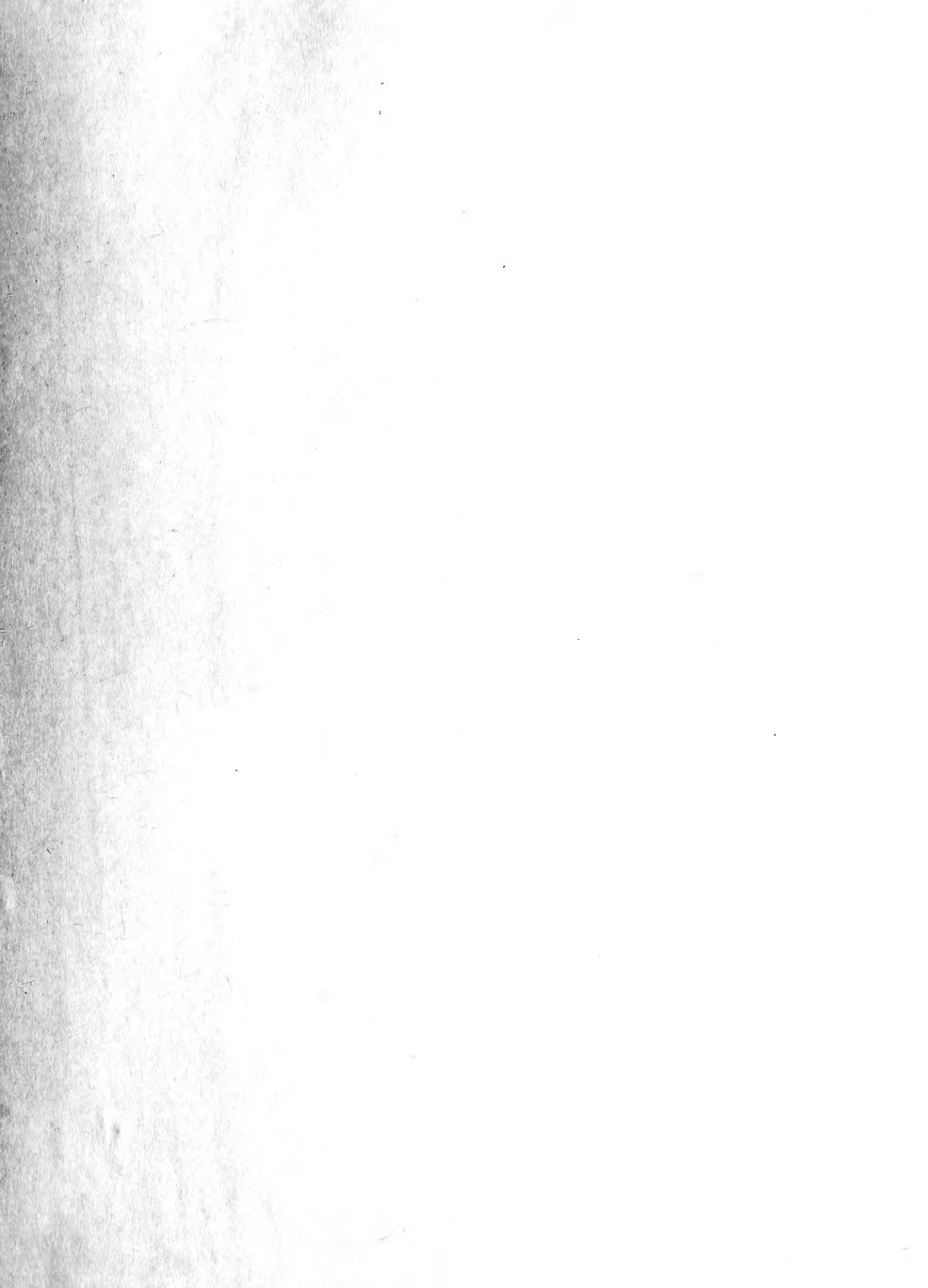
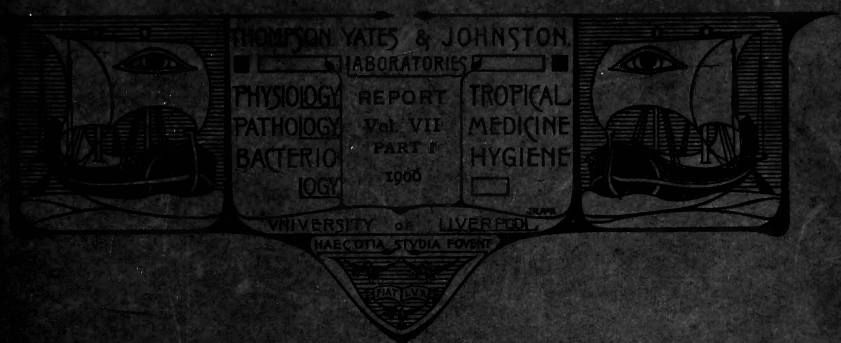


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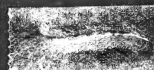
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NEW SERIES





THOMPSON YATES AND JOHNSTON
LABORATORIES REPORT



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THE THOMPSON YATES AND JOHNSTON LABORATORIES REPORT

EDITED BY

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ON A NEW PATHOGENIC LOUSE WHICH
ACTS AS THE INTERMEDIARY HOST OF A
NEW HAEMOGREGARINE IN THE BLOOD
OF THE INDIAN FIELD RAT

ON A NEW PATHOGENIC LOUSE WHICH ACTS AS THE INTERMEDIARY HOST OF A NEW HAEMOGREGARINE IN THE BLOOD OF THE INDIAN FIELD RAT

(*JERBELLUS INDICUS*)

BY

S. R. CHRISTOPHERS, M.B., (VICT.)
I.M.S., The King Institute, Guindy, Madras

AND

R. NEWSTEAD, A.L.S., F.E.S., etc.
(With one plate)

HAEMATOPINUS STEPHENSI, n.sp.

Male (fig. 1).—Body rather slender. Head as broad as long, quadrangular, posterior angles with a large flat chitinous expansion from which arises a stout hair extending backwards and reaching slightly beyond the insertion of the third pair of legs. Mentum with six short, curved spines, arranged in a circlet; beyond the mentum is a bilateral series of three larger spines, arranged somewhat in the form of a circle. Mesothorax with two long, stiff hairs, widely separated. Antennae (fig. 2) stout, of five segments; first segment much the largest, broader than long, the length equalling half the width of the head; second segment simple; third segment the shortest, anteriorly produced into a long, blunt, curved spine; fourth segment simple, not quite as long as the second; apical segment shorter than the fourth, apex truncate, bearing three or four minute spines; margins of all the joints more or less highly chitinated. Leg i. shorter than the rest; leg ii. (fig. 3) similar to leg i., but the tarsus is a little more dilated; claw long and slender; leg iii. much the stoutest; terminal clasping-claw (fig. 4) large, apex blunt; inner sub-terminal claw much smaller, and when closed lies completely hidden within a groove in the tarsal joint, a small stout spine arises from its base. Abdomen of nine segments, each segment furnished with a transverse series of long, stiff hairs, some of those at the margins being much the longest. Genital armature (see fig. 1) with a central, slightly curved, blunt, spine-shaped, or horn-shaped organ, on either side of which is a small setiferous lobe.

Female.—Head (fig. 5) much narrower than that of the male, somewhat rectangular, length greater than the width. Antenna (fig. 6) of five segments; basal segment much the widest, its length equalling about one-fourth the width of the head; second segment the longest; apical segment truncate and furnished with several minute hairs; formula 2, 1, 4 (35); margins

of all the segments highly chitinised. Legs resembling those of the male; but the tarsi of Leg i. and ii. (fig. 7) are attenuated anteriorly. Anal segment (fig. 8) with two broad, thin plates, each bearing three minute hairs.

Average length of both sexes, 1.4mm.; width, 5mm.

The larva closely resemble the adults; but the abdomen is much smaller and the hairs projecting from it are proportionately very long; the segments carry a fringe of only four hairs instead of many as in the adults.

Ovum, with a comparatively large clasping organ or pedicel; anterior pole with an irregular emarginate cap, which splits off at the period of hatching. The eggs are attached to the hair of the host at about one-third of the distance from the base, and measure approximately, .5 by .2mm.

INTERNAL ANATOMY.

Alimentary Canal.—This organ consists of the following portions :—

Fore-gut.

Mouth.

Chitinous pharyngeal pump.

Oesophagus.

Mid-gut.

1st portion or descending part of mid-gut.

2nd portion or ascending part of mid-gut.

Pyloric ampulla with the origin of malpighian tubules.

Hind-gut.

Intestine.

Rectum.

The *mouth* is very small. The opening is situated beneath the prow-like anterior portion of the head.

The pharyngeal pump is long and narrow. It passes through the head and into the thorax. It ends in the front part of the thorax in a number of chitinous bars.

The oesophagus passes backwards and upwards, surrounded by the large ganglionic masses. It is a delicate wrinkled tube, much folded upon itself. It enters the large and massive mid-gut with no appreciable proventricular fold.

The mid-gut is sharply bent upon itself, so that it forms a U-shaped organ. The first portion is the largest and its walls are thickest. It is lined by large granular cells with large nuclei. In the distended organ the cells are flattened. In the empty viscus they are cubical. Externally there are longitudinal and circular fibres arranged to form an open network. During life rythmical contractions are constantly taking place. The contents are blood, either unaltered in appearance, or partially digested. The mid-gut, especially the more massive first portion, occupies, when distended, most of the abdominal space not taken up by the ovaries.

The pyloric ampulla is a dilated portion of the mid-gut supplied with numerous circular muscles. Four malpighian tubules open into it. These

enter, two on either side, close together. Immediately beyond the malpighian tubules, a distinct dividing line between the mid-gut and the intestinal epithelium is seen.

The intestine is straight and thin-walled, but there is no differentiation into large and small intestine. The intestine passes from the muscular pyloric mass, close beneath the abdominal terga, to the rectum. The cells lining the cavity are small; there is a layer of circular muscle fibres, and outside this a number of longitudinal fibres. The nuclei of the latter form conspicuous objects in the fresh tissues. The rectum consists of a distended globular portion, containing rectal papillae, and a straight narrow portion leading directly to the anus at the apex of the 9th segment.

Salivary Glands.—These are small oval structures, consisting of a single acinus, which rests upon the anterior portion of the mid-gut in the first abdominal segment. A duct, which is of delicate structure, leads forwards towards the pharyngeal pump. Each acinus consists of several large cells with a central clear space, which is very refractile.

Malpighian tubules.—These resemble the tubules of insects generally and consist of cells with large oval nuclei. The cells are much drawn out, and nuclei are situated at considerable intervals along the tube.

Generative organs.—The female organs consist of an ovary on each side, opening into a short common oviduct. Each ovary is composed of 5 or 6 follicular tubes. Each follicular tube is attached to the body wall by a delicate apical strand of tissue, and opens into the oviduct of its own side. Each follicular tube contains two or more egg follicles in different stages of development. In the adult louse two fully matured follicles, one lying on each side, largely fill up the abdomen. All, except the youngest follicles, consist of a single layer of cubical or columnar cells surrounding an ovum and nurse cells. In the mature follicles the nurse cells, which lie towards the apex of the follicle, have become absorbed.

Spermatheca.—This is a large, thin-walled, chitinous sac, opening by a short tube near the anus. It may be empty or contain masses of spermatozoa.

Male organs.—The testes are curious double peg-top shaped organs. Each opens by a narrow tube into a wide seminal vesicle, in which masses of spermatozoa are seen. The duct of the testis opens at a distance from the end of the seminal vesicle, so that this possesses a caecal extremity. The seminal vesicle lie across the abdomen and open together into a short, straight tube surrounded with large muscle fibres. This tube in turn passes into the penis.

The fat body.—This is well developed. In the head and thorax it forms pads lying between the muscles and the organs. A very conspicuous pad lies beneath the pharynx, and other masses are situated close to the salivary glands. In the abdomen, the fat body consists of a number of conical masses attached by their apices to the body wall, near the origin of the lateral hairs. The bases of the conical masses lie against the mid-gut and other viscera and give support to these. The cells which compose the fat

body contain, as well as oil globules, masses of opaque granules, apparently of a calcareous nature.

In addition to the fat body, certain very curious cells are seen free in the body cavity. On dissecting the abdomen, these are liberated and lie about on the slide, quite unconnected with the other tissues. They are oval or spindle-shaped, measuring $140\ \mu$ in length. At one or both poles they have a delicate spike-like process. They contain two nuclei, and possess a fairly resistant cuticle, which is left as a shrunken structure when the cell contents have been extruded. In spite of the parasitic like aspect of these cells, they appear to be normal tissue cells of the louse. Somewhat similar cells, though in less numbers, were found in dissection of a species of louse infesting calves. Certain groups of small, partially free, cells are also seen in the body cavity, especially near the terminal segments. The nature of these and the large cells noted above is not clear.

Muscular system.—Powerful muscles are concerned with the pumping organ and the large antennae. These occupy much of the space in the head, which is not taken up by the large ganglia. The thorax is mainly muscular. The abdomen has certain small dorso-ventral muscle bundles, which, seen in optical section in the fresh louse, are conspicuous refractile bodies. A band of muscle passes along each side of the body, and is attached to each segment near the origin of the long hairs. In the male powerful muscles are seen in connection with the penis.

Tracheal system.—Two large spiracles of oval shape are situated just behind the spiny area of the thorax. From these, and smaller abdominal stigmata, tracheae form loops with distributing branches for the tissues. The tracheae are not very large or numerous.

Nervous system.—The ganglionic masses of the head are of great size. The thoracic ganglion is also a large and conspicuous object, especially in sections.

The circulatory system.—There is a pulsating chamber beneath the 6th and 7th abdominal terga, from which a dorsal vessel, also pulsatile, passes forwards over the mid-gut. Muscle fibres of a peculiar nature pass outwards from the chamber to the body wall.

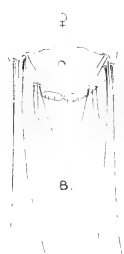
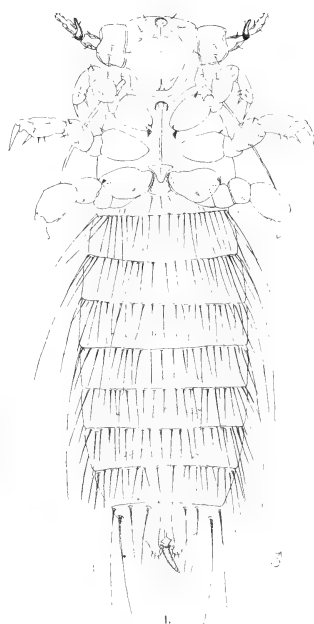
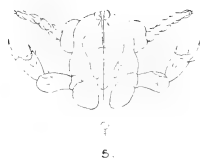
Habitat.—Parasitic on the Indian field rat (*Gerbillus indicus*), chiefly in the region of the head and shoulders; but to a less extent elsewhere. The lice are active in their habits, and evade capture, although the eyes are absent in both sexes. In this connection it may be interesting to add that their host is nocturnal in its habits and an extensive burrower.

This species is related to *Hematopinus acanthopus*, Burm.; found on the European field vole (*Arvicola* sp.) and *H. sciuropteri*, Osborne, of North America; but it is easily separable from these by the greater number of hairs on the abdominal segments, by the form and character of the hind tarsi, and the structure of the genital armature of the male.

EXPLANATION OF THE PLATE I

- Fig. 1.—Male (ventral), $\times 75$.
 Fig. 2.—Antennae of the male, $\times 150$.
 Fig. 3.—Leg ii of the male, $\times 150$.
 Fig. 4.—Tarsus of leg iii of the male, $\times 150$.
 Fig. 5.—Head of the female (ventral), $\times 75$.
 Fig. 6.—Antennae of the female, $\times 150$.
 Fig. 7.—Leg i of the female, $\times 150$.
 Fig. 8.—Anal segment of the female, $\times 75$.

PLATE.



R. Newstead del.

HÆMATOPINUS STEPHENSI, n.sp.

NOTE ON THE ANATOMY OF
GASTRODISCUS HOMINIS

NOTE ON THE ANATOMY OF *GASTRODISCUS HOMINIS*

(LEWIS AND MCCONNELL, 1876)

BY

J. W. W. STEPHENS, M.D. CANTAB.

WALTER MYERS LECTURER IN TROPICAL MEDICINE, UNIVERSITY OF LIVERPOOL

Since Lewis and McConnell,¹ in 1876, first described the anatomy of this fluke, it would appear that no subsequent examination of its structure has been made. Having found specimens of this fluke among some old post-mortem material from cases of Kala-azar, in Assam, preserved by Major Ross, I determined to re-examine this fluke, as doubts had been expressed by Leuckart² as to the correctness of some portions of Lewis and McConnell's description. I had intended, by cutting serial sections, to have investigated further several points not apparent by simple dissection. The imperfect state of preservation of the internal structures has, however, prevented my doing this completely, but I have been able to show that Leuckart's doubts were well founded, and that Lewis and McConnell's description, good as it is, is yet not accurate in some respects, and in others is incomplete. This fluke belongs to the family Paramphistomidae (Fischöeder) and to the sub-family, Cladorchinae, possessing pharyngeal pouches. The only other fluke in the genus *Gastrodiscus*, to which this species belongs, is *G. polymastos*, which has been fully described by Lejtényi³. I was able to examine sections of this latter species, and on comparing them with those of *G. hominis* it became evident that in the main their structure was the same, though differing in details, and especially, as has been noticed by others, in the different characters of their "discs."

External Features:—

Without entering into detail concerning the external characters, for these have already been described by earlier observers, it will suffice to point out that *G. hominis* has a longer anterior portion than *G. polymastos*, and has the opening of the common genital pore about the middle, while in *G. polymastos* the common genital pore lies on the border or actually within the anterior margin of the disc. Again, in *G. hominis* the posterior sucker is actually longer, and relatively to the size of the disc much larger than in *G. polymastos*. The figures given by Lewis and McConnell of the external appearance of the fluke, though quite adequate for purposes of recognition, do not, in my opinion, accurately represent the shape of the disc. This, as also in *G. polymastos*, is not bordered by a complete rim, more or less inverted, but is interrupted in front where it is in continuity with the anterior conical portion, and also behind where the cuticle covering the sucker is continuous with that covering the dorsum of the disc (fig. 1).

Alimentary Canal :—

The oral cavity, at first circular in outline, then becomes elongated transversely, as it eventually expands into the two lateral pouches (fig. 3). The whole of the wall of the buccal cavity, including the pouches, is formed of thick bundles of muscle. The oesophagus, which is the portion below the level of the pouches, leads into a well-developed sphincter muscle at the point at which the gut forks. This point is a somewhat variable one, the bifurcation taking place, as noticed by Lewis and McConnell, sometimes above and sometimes below the level of the common genital pore. From this point the gut forks diverge to run a practically straight course, terminating about the centre of the opening of the posterior sucker.

Nerve Ganglia :—

At the level of the pharyngeal pouches two prominent ganglia are seen in transverse section. From these, according to Lewis and McConnell, nerve filaments run on the ventral surface of the two gut forks.

Excretory System :—

The excretory vessels are very well developed, and, as in *G. polymastos*, extend to the apex of the anterior conical portion. They appear to be especially numerous and large on the ventral surface of the disc.

Genital Organs :—

In Lewis and McConnell's figure of the genital organs of this fluke two lobed bodies are depicted, the anterior of which was considered to be the testis, and the posterior one the ovary. Now the allied species *G. polymastos* has two testes, and the posterior one approximately in the position of this so-called ovary of *G. hominis*. This fact and the fact that a single testis had only been described in one other "Amphistome," viz., *A. subclavatum*, led Leuckart and Cobbold to doubt whether this was an ovary, and to think that the ovary had been overlooked in the dissection. This is exactly what has occurred. This posterior body of Lewis and McConnell is a testis, and not an ovary.

Testes :—

They are *two* in number (fig. 2). The anterior, which is smaller than the posterior, lies at about the level where the anterior conical portion joins the disc. It is a lobed body, and is separated from the posterior testis by some of the uterine coils. The posterior testis, also lobed, lies just in front of the anterior margin of the posterior sucker, and is separated from it by the ovary.

The vasa deferentia leave the testes on their dorsal aspect, but their exact course could not be followed. While in *G. polymastos* the one testis has a postero-lateral position with regard to the other, both occupying the area enclosed by the disc; in *G. hominis* the testes lie directly behind one another, and the anterior partly encroaches on the conical portion of the fluke. Probably connected with this is the more anterior position of the genital pore in *G. hominis*.

While the ducts could not be traced with certainty, a very striking appearance in many sections was the dilated seminal vesicle crowded with spermatozoa. This portion of the duct lay coiled for the most part transversely between the genital pore and the anterior testis.

The Ovary :—

Approximately oval in shape, and slightly constricted in the middle, is much smaller than the testis, and lies slightly to the right of the middle line between the posterior testis and sucker.

Situated dorsally, just behind the ovary, lies the well-developed shell gland. From the lower border of this Laurer's canal could be followed, opening after a short course dorsally (fig. 4). The uterine coils are situated dorsally to the testis, and could only be traced in the sections by the remains of broken-up eggs.

The Vitellaria :—

While in *G. polymastos* the vitellaria can be traced in sections as far forward as the genital pore lying external to the gut forks, and are massively developed posteriorly in the region of the sucker; in those sections of *G. hominis* which were more or less perfect the vitellaria could only be traced as far forward as the anterior border of the posterior testis. In this case also the vitellaria were most developed posteriorly in the region between the posterior sucker and the termination of the gut forks (fig. 2).

The Disc :—

The disc in *G. polymastos* is covered with numerous papillae visible to the naked eye. On the summit of these open a corresponding number of accessory suckers which, on cross section, show themselves as a number of tubes. In *G. hominis* there is no trace of these suckers. On the other hand, the cuticle over the ventral surface of the sucker is nowhere smooth as it is on the dorsum, but is thrown into a number of microscopic ridges, apparently caused by the disposition of the excretory tubules, which are very numerous in this position. These ridges are evidently not due to contractions of the cuticle, for they are quite unlike artificial papillae produced by contractions elsewhere. They show no signs of being perforated when cut transversely to the surface.

G. hominis then forms no exception to the rule that the *Paramphistomidae* possesses two testes.

I have not considered here other details, especially the structure of the genital papilla and its appendages, owing to the imperfectly preserved state of the tissues.

LITERATURE.

- (1) *Amphistoma hominis*: n.sp. A New Parasite affecting Man. By T. R. Lewis, M.B., and J. F. P. McConnell, M.B., Proc. Asiat. Soc. Bengal, 1876, p. 182.
- (2) Leuckart. Die Parasiten des Menschen, Trematodes, p. 450.
- (3) C. v. Lejtényi Ueber den bau des *Gastrodiscus polymastos* Leuckart, mit drei Tafeln. Senckenberg: Natur. Gesell. Zweolfter Bd., pp. 125-146.

EXPLANATION OF FIGURES.

Fig. 1.—Ventral view: c.g.p., common genital pore; p.s., ventral sucker; d., disc.

Fig. 2.—Schematic frontal section: ph.p., pharyngeal pouch; sph., sphincter; c.g.p., common genital pore; t.a., testis anterior; t.p., testis posterior; ov., ovary; sh.gl., shell gland; vit., vitellarium.

Fig. 3.—Transverse section through pharyngeal pouches: ph.p., pharyngeal pouch; gang., oesophageal ganglion; oes., oesophagus.

Fig. 4.—Transverse section in front of the posterior sucker: r., "ridges" on disc; ov., ovary; sh.gl., shell gland; l.c., Laurer's canal.

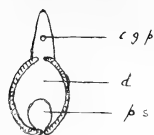


Fig 1

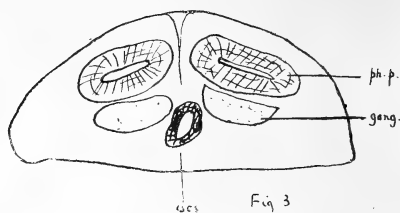


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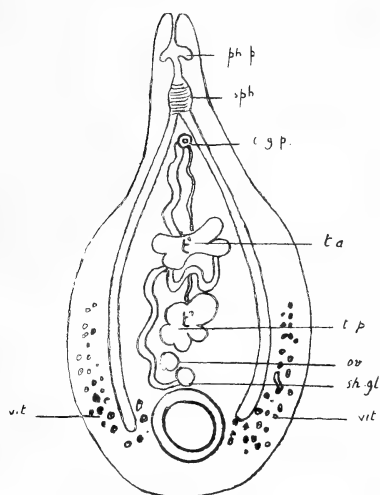


Fig 2

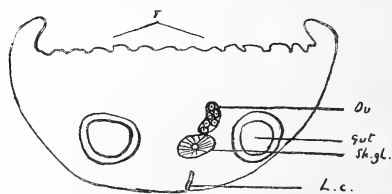


Fig 4.

A REVISION OF THE SARCOPSYLLIDAE
A FAMILY OF SIPHONAPTERA

A REVISION OF THE SARCOPSYLLIDAE A FAMILY OF SIPHONAPTERA

By KARL JORDAN, PH.D.

AND

THE HON. N. CHARLES ROTHSCHILD, M.A., F.L.S.

OVIDO, in his *Coronica de las Indias*, published in 1551, appears to be the first to have noticed the Jigger or Chigoe. This insect, which is a member of the family of fleas known as the *Sarcopsyllidae*, is the first exotic flea ever described. Travellers in the tropics of America could scarcely avoid making the acquaintance of this well-known pest, which infests both men and quadrupeds. The Chigoe is mentioned in several works of the sixteenth, seventeenth, and eighteenth centuries, CATESBY giving a figure of the animal which is easily recognised.*

LINNÉ, in 1758, described the Chigoe as *Pulex penetrans*. Apparently he did not know the insect except from the figure in CATESBY and the descriptions in several authors which he quotes. His diagnosis, *P. proboscide corporis longitudine*, is of course erroneous. This species and the human flea were the only ones LINNÉ distinguished by a name, though under the title of *Pulex irritans* he includes a number of different species, such as those from the dog, cat, fowl, rabbit, etc.

WESTWOOD, some eighty years later, makes the same error as LINNÉ did in his Latin diagnosis which we have quoted above. Some of the pre-Linnean authors—and LINNÉ himself in the first editions of his *Systema Naturae*—considered the Chigoe to be a mite, or expressed doubt as to the group into which this insect should be placed.

Even such a naturalist as OKEN held the opinion of *Pulex penetrans* being a mite, though it is only fair to add that his acquaintance with the insect was derived from books only. The first author to consider this now well-known insect to be a flea was OVIDO himself, DUMÉRIL, POHL and KOLLAR, and others following suit.

GUÉRIN, in 1838 or 39, characterised the Chigoe under a separate generic title, *Dermatophilus*, which name has to be employed instead of WESTWOOD's later one, *Sarcopsylla*. WESTWOOD when proposing his generic title in 1840, based his description upon some female specimens of this insect preserved in alcohol. The male he apparently failed to recognise with any degree of certainty, considering CATESBY's figure to represent rather an unextended female than a male. For some specimens of the *Sarcopsylla* found on a dog, which the natives considered to be different from the

* *History of Carolina*, &c. II. p. 110. tab. 10. fig. 3 (1743).

ordinary Chigoe (calling it *Bicho de Cacharro*), he proposed the name of *Sarcopsylla canis*. WESTWOOD, however, did not know this *Bicho de Cacharro*, nor did he attempt to characterize it from that report. There is no reason to believe that this *Sarcopsylla canis* is really distinct.

The Chigoe was the only species known to science as late as 1860.* FRAUENFELD, however, at this time described an allied form under the name of *Hectopsylla psittaci*, from South America, collected from a parrot.

WESTWOOD, in 1874, recorded a third member of this group under the name of *Sarcopsyllus gallinaceus*. This was the first species recorded from the Old World, and is now known to infest the domestic fowl apparently in all warm countries where the descendants of the Indian *Gallus gallus* have been introduced as domestic animals.

In 1880 a fourth species was described by HALLER, having been collected from a South American bat, under the name of *Rhynchopsyllus pulex*.

Of the last three mentioned forms, only the females were at that time known.

TASCHENBERG, in 1880, in his well-known monograph entitled *Die Flöhe*, was the first author to deal with these four fleas, and all other species of *Siphonaptera* known at that time. This monograph has been the basis for all subsequent research in this order of insects. The *Siphonaptera* are herein divided into two families, the *Sarcopsyllidae* and the *Pulicidae*. The descriptions of each family given by the author are in the main quite correct. It may here be observed that as the name *Sarcopsyllidae* is the first to have been given to the present family, and as this name is, moreover, accompanied by a diagnosis, it is necessary to employ it, though the generic title *Sarcopsylla*, as we have already stated, must unfortunately be rejected as a synonym of *Dermatophilus*.

TASCHENBERG considered that *Rhynchopsyllus pulex* and *Hectopsylla psittaci* were identical. In this, however, he was mistaken, as we shall point out in the body of this paper.

Since the appearance of TASCHENBERG's monograph four more species of the present family have been described. WEYENBERGH, in 1881, published the description of a supposed new *Hectopsylla*, which he named *testudo*. 'This insect is the same as *H. psittaci* according to some specimens from WEYENBERGH's collection. The *Echidnophaga ambulans* OLLIFF (1886), from New South Wales, is undoubtedly a *Sarcopsyllid* allied to *gallinaceus*, though OLLIFF's description is not exact enough to enable us to recognize the species with certainty. The generic term *Echidnophaga*, however, cannot be rejected for *gallinaceus* and allies. ENDERLEIN discovered and described in 1901 (*Sarcopsylla* =) *Dermatophilus caecata* which he found on a Brazilian rat, in some respects undoubtedly the most specialized *Sarcopsyllid* at present known. The fourth species was described and figured in 1903 and 1904 by TIRABOSCHI under the three names of *Sarcopsylla gallinacea* var. *murina* or *italica*, and *S. rhynchopsylla*, which he found on rats in Italy.

* For literature see the account of each species in the body of this paper.

In 1904 BAKER proposed the new generic term *Xestopsylla* for *gallinaeae*, and further separated TASCHENBERG's *Sarcopsyllidae* into two families, the *Sarcopsyllidae* (including *Dermatophilus* = *Sarcopsylla*, and *Xestopsylla*) and the *Hectopsyllidae* (including *Hectopsylla* = *Rhynchopsyllus*). BAKER was not acquainted with the *Hectopsyllidae*, knowing them only from TASCHENBERG. The family distinctions given by him do not hold good. Shortly before BAKER the genus *Argopsylla* was erected by ENDERLEIN.

From the material which we have at hand, and through the kindness of several correspondents, we have been able to examine and compare specimens of all the seven species of the present family that have been as yet described. In addition to these we propose to describe in the present article seven new species, making the total number of species of the *Sarcopsyllidae* at present known fourteen in all; the male of *psittaci* is also described here for the first time. Of the early stages of these insects we can add nothing original to what has already been published of the ova, larvae, and pupae, and therefore abstain from merely repeating what has been said by previous writers.

The *Sarcopsyllidae* are of special interest for more than one reason. These insects are in the female sex more or less stationary, fixing themselves firmly to their host and becoming true parasites. It may, therefore, naturally be expected to find peculiar modifications in their morphology, such as are always observed when a species passes from an active to a stationary life. These modifications are the more easily understood as the various species are not all stationary to the same degree. The *Sarcopsyllidae* are plainly a development from the less specialized family *Pulicidae*, in fact, the gradation in the development of the organs from a generalized to a more specialized stage is strikingly illustrated in these insects.

An account of the morphology of the *Sarcopsyllidae* and the relation of the family to other *Siphonaptera* cannot well be attempted without first referring to their classification. The peculiarities in the morphology cannot be satisfactorily explained without reference to the nomenclatorial terms under which the genera and species are referred to in this paper. The following synopsis of the *Sarcopsyllidae* in which descriptive detail treated of in the body of this paper has been omitted, will serve the purpose indicated:—

I. Family *Sarcopsyllidae* Taschenb. (1880).

Rostrum rather long but very weak, being pale and consisting of two or three segments, inclusive of the unpaired basal segment. Genal edge of head always produced downwards into a triangular process situated behind the insertion of the maxillae at the ventral oral angle. Thoracic tergites together shorter than the first abdominal tergite.

The fourteen species can be grouped into three genera, each genus being a natural division based on relationship.

1. *Dermatophilus*, with two species (*penetrans* and *caecata*), from South America, *penetrans* being also introduced into Africa.

Rostrum consisting of two segments. Head not divided by a groove or an internal thickening from the antennal groove upwards. Thoracic tergites in the dorsal line together less than half the length of the first abdominal tergite. Prosternite not produced posteriorly into a distinct conical tooth. Pygidial plate without grooves in the mesial line, each side bearing eight grooves. Hind coxa produced anteriorly at the apex into a tooth; no patch of spines on the inner side. Hind femur simple. Tibiae with three pairs of dorsal bristles. Tarsi very slender; some apical bristles of segments two, three, and four of hind tarsus very long and thin; fifth segment linear, about eight times as long as it is broad, with a few long and thin hairs; claw slender, without basal projection. Female without anal stylet and without stigma on first, second, and third abdominal tergites.

2. *Hectopsylla*, with four species (*psittaci*, *pulex*, and two sp. nov.), from South America.

Rostrum consisting of three segments. Head not divided by a groove or an internal thickening from the antennal groove upwards. Pygidial plate as in *Dermatophilus*. Abdominal tergites two to eight with a stigma in both sexes. Hind coxa without patch of spines on inner side. Hind femur produced ventrally at the base into a prominent hook, behind which the femur is deeply sinuate. Some of the bristles of the hind tibia and tarsus very long. Anal segment of female without stylet. Tergites two to eight with stigma in both sexes.

3. *Echidnophaga*, with eight species (*gallinaceus*, *murina*, *ambulans*, and five new ones), from Africa, Europe, Asia, and Australia, *gallinaceus* being introduced also into America.

Rostrum consisting of two segments. Head divided by a groove or an internal thickening from the antennal groove upwards. Abdominal tergites two to eight with a stigma in both sexes. Pygidial plate not divided in the mesial line, bearing on each side thirteen or fourteen grooves. Hind coxa anteriorly produced at the apex into a broad tooth and bearing on the inner side a patch of spines. Hind femur simple. Bristles of legs shorter than in *Hectopsylla*. Anal segment of female with stylet. Tergites two to eight with stigma in both sexes.

All the other *Siphonaptera* can be placed into two more families, according to our provisional classification:

II. Family *Pulicidae* Taschenb. (1880).

Rostrum more or less strongly chitinized, consisting of five or more segments inclusive of the unpaired basal one. Thoracical tergites together longer than first abdominal tergite. Here belong the majority of *Siphonaptera*.

III. Family *Ceratopsyllidae* Baker (1905).

Head on each side with two flaps situated at the frontal oral corner. Here belong the bat-fleas only (*Ischnopsyllus**).

There are doubtless many more species of *Sarcopsyllidae* to be discovered. It may therefore ultimately be found necessary to divide the family into more than three genera. There is, however, at present no need at all for further division. By keeping such species, for instance, as *Hectopsylla psittaci* and *pulex* each in a separate genus, and proposing new genera for some of the other species which are similarly different, the natural division of the family into three sharply defined groups of species would only be obscured and no legitimate purpose served.

Though there is a great diversity among the species of *Sarcopsyllidae* in general appearance as well as in the details of structure, the family is so well characterized that one cannot possibly have any doubt about a flea belonging to this family or not. It is true, there are several peculiar characters which the *Sarcopsyllidae* share with certain other fleas, for instance, the swelling of the abdomen of the pregnant females and the loss of the basal projection of the tarsal claws. However, the remarkable reduction of the rostrum (labium and labial palpi), not in length but in chitinization and segmentation, is nowhere else observed, nor are the thoracic tergites anywhere so much reduced as in this family. The similarities existing between the *Sarcopsyllidae* and members of the second (or central) family of *Siphonaptera*, the *Pulicidae*, are such as to render it practically certain that the similarities are partly the outcome of convergent development and partly indications of blood-relationship between the *Sarcopsyllidae* and the *Pulicidae*. This is, in our opinion, best demonstrated by a general comparative description of the morphology of these insects.

The head of the *Siphonaptera* is divided by the antennal groove into an anterior or frontal portion (hereafter referred to as the frons) and a posterior or occipital portion (hereafter referred to as the occiput). The antennal groove is usually prolonged dorsally as a narrow slit in the ♂♂ of *Siphonaptera*, the grooves of the two sides of the head often meeting on the top. There is normally also an internal incrustation of the skeleton from the groove upwards in both sexes. This arrangement is well marked in the *Sarcopsyllid* genus *Echidnophaga*. In the genera *Hectopsylla* and *Dermatophilus* the dorsal prolongation of the antennal groove and the internal thickening of the chitin are absent in both sexes, the genera *Dermatophilus* and *Hectopsylla* being in this respect more specialized than *Echidnophaga*. Such a specialization is not confined to these two genera of *Sarcopsyllidae*. We meet with it also among the *Pulicidae* in the genera *Cbaetopsylla* and *Vermipsylla*.

The frons and the occiput of the *Sarcopsyllids* (Pl. I, Fig. 1-5), like those of the true *Pulicids*, bear dorsally and dorso-laterally a number of deep punctures, each puncture being provided with a short hair.

* WESTWOOD, *Entom. Magaz.*, i. p. 362 (1833) (nom. indescr.); id., *Intr. Classif. Ins.*, ii., *Syn.* p. 125 (1840).

The frons bears only two bristles of any length, the one standing before the eye and the other near the insertion of the maxillary palpus, a small hair being placed between or above them. These bristles are constant in number in the genera *Echidnophaga* and *Hectopsylla*, but the eye-bristle is placed a little higher in the latter genus than in the former. In the two species of *Dermatophilus* these bristles are much reduced or even absent. The position of the eye-bristle in front of the eye is a generalized character present in the majority of fleas. Only a few of the true *Pulicidae*, namely *irritans** and its close allies, have the eye-bristle beneath the eye. The Sarcopsyllids having kept the original position of the bristle it is beyond doubt that they are not derived from a form identical with the present day *irritans*. The frontal bristles are most developed in *E. gallinaceus*.

The occiput normally bears three rows of bristles in the *Siphonaptera*. The first row is placed behind the base of the antennal groove (where the antenna is inserted), the second, or median, row in the centre of the side, and the third or subapical, row near the hinder edge of the head. There are frequently intermediate bristles as well, more or less arranged in rows. The most ventral bristle of the subapical row is everywhere the longest occipital bristle. Among the *Sarcopsyllidae* all the three normal rows are represented in the genus *Hectopsylla* only, the other genera presenting all grades of reduction in the number of the bristles down to almost total disappearance.

The ♂ of *Hectopsylla psittaci* exhibits the largest number of occipital bristles in the most normal position. In this ♂ we find two bristles near the base of the antennal groove, two or three in the middle of the side, and three or four near the hinder edge. The ♀ of this species has practically the same number of bristles, but a curious shifting of the last row may be observed. The most ventral bristle of this row retains its normal position, but the other subapical bristles, or at least some of them, are more or less moved forward so as to form a single row with the median bristles. The subapical row, therefore, appears to consist in this ♀ usually of one bristle only, mostly accompanied by a small hair, there being occasionally an additional long bristle above the antennal groove, making four in all of such supra-antennal bristles. The bristles of the occiput are similarly placed in both sexes of *Hectopsylla coniger*, and in the ♀♀ of *Hectopsylla broscus* and *pulex*, of which the ♂♂ are not known. From an examination of these last three species alone it might be erroneously concluded that the subapical row of bristles was practically absent. None of the other *Sarcopsyllidae* have three long bristles immediately above the antennal groove, the bristles of the anterior row being either absent or represented by minute hairs. The median bristle and the subapical one remain relatively long in *Echidnophaga gallinaceus*, *murina*, and a new species, while only the subapical one is well developed in the other species of *Echidnophaga*. In *Dermatophilus* this last bristle is also small, there being in this genus, moreover, only a few tiny hairs belonging to the median and subapical rows.

* A list of the Siphonaptera referred to in this introduction will be found at the end of the introduction.

The row of short hairs so often found along the antennal groove in many of the *Pulicidae*, especially in the ♂♂, is absent in the *Sarcopsyllids*.

The majority of the *Pulicidae* have the genal edge of the frons armed with a comb of long teeth (genal comb), which the specimens, judging from live individuals put in cotton wool, apparently use in moving through the fur of the host. This comb is absent from the greater number of species of the genus *Pulex*, for instance, from *P. pallidus*, *cleopatrae*, *bohlsi*, etc., while in *Pulex irritans* the comb is usually represented by one or two very small teeth only, which are often absent. In two of the species of *Pulicidae* known to us the comb appears to be replaced functionally, not morphologically, by one large tooth-like projection, the prolongation of the post-oral angle formed by the oral and genal edges. This post-oral process is found in *Lycopsylla novus* and in *Pulex riggenbachii*. In *Ctenophthalmus wernmanni* there are two genal spines above a small post-oral process. All the *Sarcopsyllidae* without exception possess a large triangular post-oral process, which is more or less curved backwards (Pl. I, Fig. 1-5). This hook resembles the conical projection into which the prosternite is prolonged. A similar projection is met with in the ♀♀ of *Hectopsylla coniger* and *brosus* on the episternum of the metathorax, while the metathoracic epimerum bears dorsally also a similar, but curved, process (Pl. I, Fig. 5). These processes, as well as a lateral lobe of the hind margin of the occiput of the ♀ of *Echidnophaga gallinaceus*, have all doubtless the function of helping to prevent the specimen from slipping back when pushing itself through the fur or feathers of the host. The two lobes which are placed on each side of the head at the frontal oral angle in all *Ceratopsyllidae* (bat-fleas) serve presumably the same purpose, but are not homologous to the post-oral lobe of the *Sarcopsyllidae*, and of the few *Pulicidae* mentioned above. It is significant that similar processes are found on the thoracic pleurae in *Malacopsylla*, the ♀♀ of which genus fix themselves permanently (or at least for a longer period) on their host, resembling in this respect the ♀♀ of *Sarcopsyllidae*. In the likewise stationary *Vermipsylla alacurt* there are no such processes.

The peculiarities in the structure of the caputal capsule cannot be well discussed without reference to one of the most conspicuous features in the organization of the *Sarcopsyllidae*, the enormous reduction of the thoracic tergites. This reduction, which we find already indicated to a small extent among the *Pulicidae* in *Pulex irritans* and *leporis*, and the members of the genus *Malacopsylla*, but not in the genera *Vermipsylla* and *Cbaetopsylla*, is not present to the same degree in all *Sarcopsyllids*, the tergites being much longer for instance in *Echidnophaga bradyi* than in the species of the genus *Dermatophilus*. As the reduction of the tergites is not accompanied by a correspondingly marked decrease of the sternites, the reduction must naturally have an effect on the shape of the head. The *Sarcopsyllidae* follow in this respect two distinct lines of development, which we must consider separately. The stages of

these two different lines of evolution are represented on the one hand by the species of the genera *Hectopsylla* and *Dermatophilus*, and on the other by the species of the genus *Echidnophaga*.

In consequence of the great dorsal reduction of the thorax, the distance from the anterior edge of the prosternum to the anterior edge of the prothoracical tergite is longer than is ordinarily the case in *Siphonaptera*. The head, being adapted to this modification, has grown backwards in *Dermatophilus* and *Hectopsylla*, its hinder and genal edges having become oblique. This has had the effect of pushing the mouth upwards, making it subterminal, and therefore the dorsal line of the head more flat than in the *Siphonaptera* with subventral mouth. This development is most pronounced in *Dermatophilus*. The piercing organs of the mouth (labrum and mandibles) which are normally directed obliquely downwards in the *Siphonaptera*, have here assumed another position, being directed obliquely forward.

Now, in *Echidnophaga* the same result is attained in another way. In this genus the reduction in length observed in the thorax takes place also in the occiput.

The relative length of the frons and occiput is variable in *Siphonaptera*. In the family *Pulicidae* the frons is as long as, or shorter than, the occiput; the opposite, however, is also found in several species. In the Sarcopsyllids the occiput appears to be never longer than the frons, it being shorter than the frons in all *Echidnophaga* and also a little shorter than the frons in *Hectopsylla*. The occiput is shortest in *Echidnophaga gallinaceus* and its close allies. The difference in length is due to a reduction of the occiput, not to an enlargement of the frons. The reduction proceeds from the hinder edge of the occiput, as seems to us to be indicated by the outline of this edge. In the *Pulicidae* this edge is always entire, being somewhat curved ventrally at the antennal groove, and more or less straight further upwards. The strongly slanting occipital edge of *Hectopsylla* and *Dermatophilus* is also entire. In *Echidnophaga*, however, especially in the species with short occiput, the hinder edge of the latter is more or less convex in the middle, the occiput being more reduced in length dorsally and ventrally than in the middle, the edge being left standing here. This convex portion is, in the ♀ of *Echidnophaga gallinaceus* and some other species, concentrated, as it were, to a prominent lateral lobe, already referred to above (Pl. I, Fig. 1 and 2). Now, the reduction of the occiput has a peculiar influence on the development of the frons. As the hinder edge of the occiput and the genal edge of the frons meet behind the antennal groove, it is obvious that the shortening of the occiput must be accompanied by an alteration in the direction of the genal edge. This edge has assumed a more oblique position than it originally had in *Siphonaptera*, and the oral edge has correspondingly become longer. In consequence of this enlargement of the oral edge the mouthparts are further away from the prosternum and forecoxae than they would normally be, if the shortening of the occiput had not been counteracted by the enlargement of the oral edge.

This forward movement of the mouth in the *Sarcopsyllidae* may, we think, be connected with the assumption of a stationary life on the part of the ♀♀. It is probable that the *Siphonaptera* which fasten themselves permanently to the skin of their host do it in a manner similar to that employed by ticks and mites, with the mouth-parts more or less in a line with the longitudinal axis of the body. This attitude appears to be assumed more or less by the ♀♀ of all the Sarcopsyllids, the ♀♀ of *Dermatophilus* going right into the skin of their host. Another morphological peculiarity is connected with this tick-like position of the parasite. The maxillary palpi are inserted close to the corner of the oral edge of the frons in the *Pulicidae*, the piercing organs projecting downward behind or in between the palpi. In the Sarcopsyllids, however, the oral slit of the caputal capsule is more or less extended upwards beyond the insertion of the maxillary palpi, the piercing organs (mandibles and upperlip) protruding, therefore, in this family in front of the palpi in the more specialized species, *Echidnophaga bradyi* being the most generalized species, in which this development has hardly begun. The frontal corner of the mouth does not project downwards as in the *Pulicidae*, except in the most generalised *Echidnophaga*, this corner being more obtuse than in the *Pulicidae*, whereby greater freedom is given to the mandibles and labrum.

There is another modification which has been evolved, we think, in connexion with the acquirement of a tick-like terminal fixation to the host; that is the angulated dorsal edge of the frons prevalent among the Sarcopsyllids. The dorsal edge of the frons of the *Siphonaptera* is normally rounded to a more or less high degree, the curvature being sometimes so strong that the mouth is thrown backwards (as in the genus *Ctenopsyllus*). The stronger the convexity of the dorsal edge of the frons is, the less easy would be a fixation to the host in the manner of mites, the projecting supra-oral portion of the frons being in the way. Where the dorsal edge of the frons is arched in side-view among the Sarcopsyllids the curvature is slight (*Hectopsylla pulex*, Pl. I, Fig. 4). This simple slight curvature, which we meet also among the *Pulicidae*, appears to us to be original, the angulated dorsal edge of the frons representing a higher specialization. The angulation is accompanied by a semicircular depression posterior of the angle, and becomes the more marked the deeper the impression is. Such a horseshoe-shaped depression occurs apparently nowhere else among *Siphonaptera*.

The edge of the depression is sometimes divided anteriorly in the middle, appearing in a side-view as two tubercles, for instance in *Echidnophaga liopus* (Pl. I, Fig. 2). These tubercles are not homologous to the frontal tubercles so commonly found in *Pulicidae*. They are doubtless acquired subsequent to the acquirement of the frontal depression.

The obtusity of the supra-oral portion of the frons, which gives the head the appearance of being truncate, has doubtless yet another meaning besides allowing the piercing organs to be thrown out almost horizontally. As the Sarcopsyllid ♀♀ fix

themselves on the skin of the host by means of the mouthparts, it is doubtless a great support to these organs that the head is firmly pressed against the skin of the host, lessening the strain on the mandibles and labrum when the host is trying to get rid of the parasite by scratching. It is easy to conjecture the line of evolution on which the head developed from a help to the organs of fixation into an organ of fixation itself. This is well illustrated by the species of the genus *Dermatophilus*. In these insects the sharp angle of the dorsal frontal edge stands close to the frontal oral corner. This portion of the head is, we think, employed either for widening the hole made by the piercing organs or for penetrating direct into the skin, the sharp angle acting in either case as a hook. In a similar way the tubercles of *Echidnophaga* (Pl. I, Fig. 1, 2) may help to fix the parasite more firmly when the skin of the host becomes irritated and swollen, and therefore more easily penetrated. The swollen skin of the host partly envelops the frons, as we know from *E. gallinaceus*.

In the genus *Hectopsylla* the dorsal horseshoe-shaped depression of the frons is absent. The heads of the species of this genus, moreover, have another characteristic not represented in the species of the genera *Echidnophaga* and *Dermatophilus*. This is a dorsal internal incrassation between the frontal oral corner and the antennal groove (Pl. I, Fig. 4, 5). This thickening is not met with in the two other genera. The same kind of incrassation—which serves as a point of insertion for muscles—is also found in the family *Pulicidae*, but here also in a few of the species only, such as *Pulex cleopontis*, *australis*, *bohlsi*, and a few others. It is worthy of remark that these species are American, like *Hectopsylla*. We must, however, add that some small American species of the genus *Pulex* (for instance *simonsi* and *cocyti*) are devoid of this incrassation, as are the members of the genus *Pulex* from the Old World. Now, does the similarity in this character between the genus *Hectopsylla* and these American species of the genus *Pulex* indicate relationship or convergent development? It is obvious that a curious instance of non-mimetic similarity between species of the same country is here represented. The incrassation is not present in the American genus *Malacopsylla*, and the old-world genera *Vermipsylla* and *Lycopsylla*, which are also probably derivations from *Pulex*.

The eye is present in all the *Sarcopsyllidae*, though its pigment is much reduced (or absent?) in *Dermatophilus caecata*. It is placed about midway between the dorsal and ventral edges of the head. This seems to be the normal position of the eye in *Siphonaptera*, though it is sometimes placed more dorsal and sometimes more ventral. In the *Sarcopsyllidae* as in the *Pulicidae* there is a marked difference among the various genera and species in the relative distance of the eye from the antennal groove. When viewed in optical section the eye is always placed immediately at the groove, but externally the eye is often separated from the groove by a strip of chitin. In the genus *Hectopsylla* this is well demonstrated (Pl. I, Fig. 3, 4, and 5), and among the *Pulicidae* in *Pulex irritans*, *Ctenocephalus canis* and *felis*, and some other species. In

some *Echidnophaga* (for instance in *E. macronychia* and *E. gallinaceus*) the eye is placed but little nearer the groove than it is in *Hectopsylla*, or rather the strip of chitin separating it from the groove is but little narrower. In *Echidnophaga larina* and *bradyta*, however, the eye approaches the groove closely, while in *Dermatophilus* it is also placed near the groove (Fig. G). As this apparent difference in the position of the eye depends on the development of the anterior edge of the antennal groove, there is a corresponding difference in the size of the latter, the groove being larger in those species whose eyes stand at the groove than in those in which the groove is covered to a greater extent by the more developed anterior edge.

The antennal groove in the *Sarcopsyllidae* is open behind as it is in the genus *Pulex*, the hinder edge of the occiput not being sufficiently raised behind the groove as to being contiguous with the genal lobe (Pl. I, Fig. 1-5). In *Echidnophaga larina*, however, that edge is so much elevated as to practically close the groove. The space between the genal lobe and the occiput is in *Pulex* filled in by the prosternite, the genal lobe being very short. A similar structure obtains in *Dermatophilus* (Fig. G), while in *Hectopsylla* and *Echidnophaga* the genal lobe is so long—or has become secondarily so much prolonged—as to separate more or less completely the prosternite from the antennal groove, as is the case also in *Ctenocephalus canis* and *felis*.

The antennae of the *Sarcopsyllidae* resemble very closely those of *Pulex pallidus*, *cleopatrae*, and some other African species. The second segment is strongly asymmetrical as in those species, being produced apically into a large obtuse projection. On this projection we find in *Echidnophaga* as in *Pulex pallidus*, *irritans*, and others a number of long bristles of about equal length, while in *Hectopsylla* there is one long bristle accompanied by several somewhat shorter ones, *Dermatophilus* agreeing closely with *Echidnophaga*, except in the bristles being thinner. The club of the antennae is connected with the second segment by a short conical stalk, the third segment. The club consists of eight segments as in other *Siphonaptera*. It shows in the *Sarcopsyllidae* a conspicuous specialization, also present in *Pulex pallidus*, *cleopatrae*, *nubicus*, etc. In these two groups of species the segmentation of the club is entirely restricted to the posterior side, there being no indication of segmentation on the anterior side. *Pulex irritans*, *Ctenocephalus canis*, and *felis* somewhat resemble *Pulex pallidus* and the *Sarcopsyllids* in the fusion of the segments of the club, the segmentation being in these species faint but visible on the anterior side of the club. The club of the species of the genera *Vermipsylla*, *Cbaetopsylla*, *Lycopsylla* and *Malacopsylla* is completely segmented as in *Pulex cleopontis*, *leporis*, etc., no other *Siphonaptera* having attained such a high degree of fusion in the segments of the antennal club as the *Sarcopsyllidae* and the Old World species of the genus *Pulex* allied to *pallidus* and *cleopatrae*.

In *Echidnophaga* the solid anterior side of the club bears a row of usually three short hairs with another short hair placed below, as is the case in *Pulex pallidus* and

its allies. *Dermatophilus* has seldom as many as four hairs similarly placed. These hairs are completely lost in *Hectopsylla*. There is no obvious sexual difference in the antennae of the Sarcopsyllids as is so often the case in *Pulicidae*, especially in *Ceratophyllus*. The antennae, however, of *Hectopsylla* on the one hand, and *Dermatophilus* and *Ecbidinophaga* on the other differ somewhat in the shape of the club, the club being distinctly longer in *Hectopsylla* than in the other genera, *Ecbidinophaga bradyta* approaching *Hectopsylla* in this respect.

One of the most singular features in the morphology of *Sarcopsyllidae* is the peculiar development of the mouth-parts. These organs are modified in a characteristic way not observed outside the family.

Here, as in other *Siphonaptera*, the mandibles are piercing organs penetrating the skin of the host, the upper lip serving as a sucking tube. While in ordinary *Siphonaptera* these organs are retracted after sucking, they remain fastened in the skin, apparently permanently, in the case of the ♀♀ of the *Sarcopsyllidae*. The piercing organs of the *Sarcopsyllidae* are much broader, and the serration of the mandibles is much heavier than in the case of other fleas, including such fleas as *Vermipsylla*, *Malacopsylla*, etc., of which the ♀♀ are more or less stationary. The mandibles are widest near the base. Their enlargement in both sexes is connected with the method of fixation on the host. The *Siphonaptera* have two main organs of fixation, the legs and the piercing organs, the extreme developments of which are represented by *Malacopsylla* on the one hand, and by the *Sarcopsyllidae* on the other, and we observe accordingly two lines of development. In *Malacopsylla* we have comparatively weak and short piercing organs, while the claws and the bristles of the legs are very strongly developed, enabling the specimens to fix themselves firmly on the host. In the *Sarcopsyllidae*, on the other hand, the legs are practically useless for that purpose, at least in the more specialized forms, the bristles and claws being very thin. In this family the mandibles serve the purpose of the claws, the specimens (♀♀) being fixed on the host by means of these piercing organs. The legs of the *Sarcopsyllidae* are often torn off and mutilated, doubtless by the host when trying to pick the parasites off. This being so, one might be justified to conclude that the strong development of the mandibles is a consequence of the assumption of a stationary life on the part of the ♀♀, the ♂♂ having inherited the same strong organs of fixation from the ♀♀, though the enlargement is unnecessary in this sex, not being stationary like the ♀♀.

Among the *Pulicidae* the species which comes nearest to the Sarcopsyllids in the width of the mandibles and the strength of the serration is *Pulex irritans*. The mandibles are not of the same size in all the *Sarcopsyllidae*, being least enlarged in *Hectopsylla coniger*. In this species of *Hectopsylla* as well as in *H. psittaci* and *bruscus*, the serration of the mandibles does not extend to the base.

The maxillae are triangular, as in the *Pulicidae*. They vary a good deal in outline in the different species. They are, for instance, long, sharply-pointed, and curved

backwards in *Hectopsylla pulex* (Pl. I, Fig. 4), while they are much more obtuse and curved forward in *H. psittaci* (Pl. I, Fig. 3). The maxillae are not piercing organs. They merely protect the mandibles and upperlip, and push aside the hairs of the host. The maxillary palpus consists of four segments, as in other *Siphonaptera*. The first segment is at least as long as the second, being often considerably longer. It is also usually distinctly curved near the base. The palpus is much more hairy in *Dermatophilus penetrans* than in the other species of *Sarcopsyllidae*.

The rostrum consists in *Siphonaptera* of an unpaired underlip and the labial palpi. It is again strangely modified in the *Sarcopsyllidae*. The rostrum is very feebly chitinized, being of a more or less white colour, and has almost lost the segmentation (Pl. I, Fig. 1 and 4). There is always one joint in the labial palpus, not more, and the joint between the palpus and the underlip has either disappeared (as in *Echidnophaga* and *Dermatophilus*), or may be present (as in *Hectopsylla*). We are not sure if the latter joint is present in all specimens of *Hectopsylla*; there may be some variability in this respect. The rostrum has not become reduced in length. In the other *Siphonaptera* the labial palpus consist at least of four segments. The labial palpi form together a kind of sheath enveloping the mandibles and the upperlip. This sheath is *not* a piercing organ, but only guides the mandibles and upperlip. This can be readily seen if a flea is placed on the hand and observed under a lens. A *Pulex* or *Ceratophyllus* if hungry will generally take readily to man, though a bird or rat flea appears to be rather disgusted with a human host, retracting the piercing organs hastily as a rule when the blood is first tasted, and not sucking for so long a time as do *Pulex irritans* and *Ctenocephalus canis* and *felis* under the same circumstances. When the insect has selected a point where to pierce the skin, the rostrum, with the mandibles and upperlip inside it, is moved a little forward. The specimen then lifts the abdomen upwards and presses the piercing organs down into the skin, using its own weight and the strength of the fore and mid legs, the hind legs being lifted up. The head can soon be seen to come nearer the skin, and the rostrum then divides in the middle, the two labial palpi remaining together only at the tip. The nearer the head comes to the skin of the host, *i.e.*, the deeper the upperlip and mandibles penetrate into the skin, the further are the labial palpi separated from one another, till they are finally quite apart, lying right and left on the skin of the host, but assuming again their normal position close to one another as soon as the insect retracts the mandibles and upperlip from the host. This retraction is done forcibly, as the action of the legs indicates during the process; the organs come out with a jerk. Now, from this short description of the method of sucking on the part of a *Pulex*, it is clear that the specimen, in the act of piercing the skin, has to overcome the rigidity of the rostrum as well as the resistance of the skin of the host, and further that, when sucking, the specimen has to use a certain amount of force to counteract the spring-like action of the labial palpi. Therefore it is conceivable that the rigidity of the labial palpi has

been lost in the *Sarcopsyllidae* in consequence of the ♀♀ fixing themselves permanently on the host by means of the mandibles and upperlip. As already described by ENDERLEIN, the labial palpi of the *Sarcopsyllidae* which are attached to the host, are lying on each side of the head and point upwards. We have observed this position in *Echidnophaga* and *Hectopsylla*. FRAUENFELD mistook the labial palpi for pale bristles. In all ♂♂ of the *Sarcopsyllidae* and in the ♀♀ which are unattached to their host, the labial palpi are directed downwards and form a sheath for the mandibles and upperlip as in other *Siphonaptera*.

The great loss of segmentation in the rostrum is doubtless secondary to the reduction of the chitization, as a long and strongly chitinated rostrum with only one or two joints in it would offer too much resistance when the piercing organs are pushed into the skin. The labial palpi of the *Pulicidae* consist normally of five segments, the number being reduced in true *Pulex*, while in some American *Pulex* (for instance in *Pulex cleophontis*) there are six segments. Some stationary *Pulicidae* like *Vermipsylla* and the Bear-fleas have more segments. This is interesting, for in these insects greater segmentation lessens the rigidity of the long rostrum, as reduced chitination does in *Sarcopsyllidae*. The greater number of segments occurs in *Vermipsylla*. The labial palpi of *Malacopsylla* consist of five short segments.

We have already referred cursorily to the great reduction of the thoracic segments which is observed in all the *Sarcopsyllidae*. All the portions of the thorax are reduced to a great extent, with the exception of the prosternite and metathoracic epimerum. The value for the individual of this contraction of the thorax is obvious. The abdomen of a *Sarcopsyllid* specimen which is fixed on or in the skin of the host does not project so much as it would were the thorax of normal length. The parasite is therefore less likely to be rubbed off by the host. It might further be argued that, as the swollen abdomen of the pregnant ♀ so presses against the thoracic tergites that they telescope into one another, a long thorax would be much in the way. A third reason, of a less speculative nature, for the reduction of the thorax, is the loss or reduction of the power of jumping, and hence a reduction of the muscles in the thorax. In the genus *Dermatophilus* the thorax is so short that the occiput almost touches the abdomen, even in non-pregnant ♀♀.

The dorsal and ventral parts of the thorax are best considered separately. The three thoracic tergites, which are together always shorter than the first abdominal tergite, bear only a remnant of the rows of bristles normally present in *Siphonaptera*. In the *Sarcopsyllidae* each tergite bears a small number of thin bristles placed in a verticle row, which row corresponds to the posterior row of bristles present in other *Siphonaptera*. On the mesonotum these bristles are much reduced in number, but there are often one or two minute hairs in front of the row, these hairs representing another row. This second row is frequently met with in *Siphonaptera*, but is seldom present on the prothorax. The presence of two rows of bristles on the tergites may

be called normal for *Siphonaptera*, though many species bear more than two. Those species, however, whose tergites have but one row of bristles only, are doubtless derived from species whose tergites had originally two rows, the anterior row having disappeared. In the *Sarcopsyllidae* the loss of bristles may be due to the reduction of the segments. In other *Siphonaptera*, however, this is not necessarily the case, the anterior row being often lost, though the tergite remains normal, as for instance in *Pulex riggenbachi*. The uniseriate bristles are the rule in the genus *Pulex*, a second row being developed only in forms which, though classified with *Pulex irritans*, are not true *Pulex*; for, instance the American species *cleophontis*, *bohlsi*, etc. The thoracic bristles of the *Sarcopsyllidae* are nearly all short, those of the metanotum being usually minute. The most ventral bristles of the pro- and mesothorax are the longest. There is no indication of a comb, nor are there any subapical hairlike spines on the meso- and metanotum, such as are present in most *Pulicidae*.

The prosternite is less reduced than the mesosternite. Its pleural plate is oblique in position, owing to the slanting genal edge of the head. This plate always ends in an obtuse lobe which projects backwards and a little sideways. The mesosternite, which is short, has a more or less vertical position, and its ventral portion (the sternum) projects but slightly forward. There is always near the upper edge of the mesosternite one fairly long bristle, rarely accompanied by a minute hair. The smallest number of bristles on the mesosternite of *Pulicidae* is two, as is the case in *Pulex irritans*, all the other *Pulicidae* having at least three long bristles in this position. The mesosternite of *Pulex irritans* has another character in which it differs from the other *Pulicidae* and in which it agrees with the *Sarcopsyllidae*. The mesosternite of *Siphonaptera* is divided by a suture extending from the insertion of

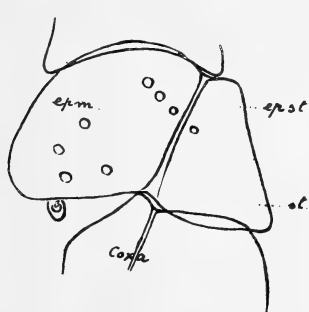


FIG. A



FIG. B



FIG. C

the coxa to the dorsal edge of the mesosternite, the suture ending usually at the upper frontal corner of the mesosternite. This suture separates the lateral portion of the mesosternite into an anterior plate, the sternum, and a posterior plate, the epimerum (Fig. A). The sternum is completely fused with the episternum, the upper portion

of the 'sternum' being, in fact, the episternum. In *Pulex irritans*, however, the epimerum is not separated from the sternum, the suture referred to being absent (Fig. B). There is also no internal thickening of the skeleton corresponding to the suture. A similar fusion of the plates is found in all *Sarcopsyllidae* (Fig. C). All the other *Syphonaptera* have the 'meral' suture separating the mesosternum of the mesosternite from the mesomerum.

The hinder edge of the mesosternite is produced into a rounded lobe similar to that of the prosternite, but usually less heavily chitinized. This lobe is present in all species of the genus *Hectopsylla*, but is not so well developed in *Dermatophilus* and *Echidnophaga*. A similar lobe is found on the metasternite of *Hectopsylla*, here the episternum being produced. In the ♂ of *H. psittaci*, however, this is not the case; while in ♀♀ of *Hectopsylla coniger* and *bruscus* also the epimerum bears a lobe (Pl. I, Fig. 5).

From the great similarity in the development of the mesosternites of *Pulex irritans* and the *Sarcopsyllids*, an equally great similarity might be expected to be present in the structure of the metasternites of these insects. This is not the case. In the true *Pulex*, namely *irritans* and *leporis* as well as in *Pulex pallidus*, *cleopatrae*, etc., there is at least one very striking peculiarity which is not found in the *Sarcopsyllidae*. In these members of the genus *Pulex* the episternum and the sternum of the metathorax are not completely separated from one another by a suture as is the case in nearly all other *Syphonaptera*, but are fused together anteriorly, the suture not extending to the anterior edge of the plate. The only other *Syphonapteron* in which a similar fusion has taken place is, as far as we know, the American *Ceratophyllus charlottensis*. In the American species of the genus *Pulex*, as well as in *Malacopsylla*, *Lycopsylla*, and *Vermipsylla*, the episternum of the metasternite is separate. There is, however, a point of resemblance between the genus *Pulex* and the *Sarcopsyllids* in the size of the episternum and sternum of the metathorax; the former being comparatively large and the latter small. The metathoracic epimerum of those *Sarcopsyllids* which are the least specialized in respect to this plate has essentially the same shape as that of the genus *Pulex*. It is long in a dorso-ventral direction, being hardly broader in *Hectopsylla* than in *Pulex*. It has become much enlarged in *Dermatophilus*. This enlargement has probably taken place in connexion with the acquirement of the distended abdomen of the pregnant female. The metathoracic epimerum serves as a basal side-plate to the abdomen covering the proximal tergites and the proximal sternites laterally where they become separated when the abdomen of the individual gets distended.

The bristles on the metasternite do not offer a character distinctive of the whole family of *Sarcopsyllidae*, but they are nevertheless of interest, inasmuch as they represent various degrees of reduction. The metathoracic sternum bears in the *Pulicidae* one bristle, seldom more, standing near the upper edge rather close to the

meral suture. This bristle is absent in *Malacopsylla*. The episternum also bears, as a rule, one or more bristles. In the genus *Lycopsylla*, however, there are no bristles on this plate. *Pulex irritans*, *leporis*, *pallidus*, etc., have a bristle on the sternum and one or more on the episternum. In the family *Sarcopsyllidae* there is one comparatively small bristle on the sternum of *Hectopsylla* and a minute one on the episternum. The species of the genus *Dermatophilus* have only a minute bristle on the sternum, whilst there is no bristle at all on either the sternum or the episternum of the metathorax of *Echidnophaga*, the last genus being in this respect the most highly specialised of the three. The bristles of the metathoracic epimerum resemble those of the genus *Pulex* in their arrangement. In the species with the largest number of bristles on this epimerum there is a row of bristles extending from the stigma downwards towards the middle, a solitary bristle being sometimes placed further ventrad. There are apparently never more than six bristles placed in this position, which is the case in *Hectopsylla Pulex*. Occasionally one or two bristles are placed in front of the normal row, these being a vestige of the anterior row of bristles commonly found in the genus *Pulex*. In some species of the genus *Echidnophaga* the number of bristles is reduced to two. In contradistinction to the Sarcopsyllids the species of the genera *Vermipsylla* and *Chaetopsylla* have the bristles of the thorax developed in great profusion.

The abdomen consists of the same number of segments as in other *Siphonaptera*. In the ♂♂ and the non-pregnant ♀♀ it appears rather short, the segments being, as in *Pulex irritans*, strongly developed in a vertical direction. Apart from the extension of the ♀ abdomen, there are some other sexual differences. The ♂ is less convex dorsally than the ♀, though more so than is the case in the ♂♂ of other *Siphonaptera*. The bristles are also not always alike in number and length in the two sexes, their number being usually less reduced in the ♂ than in the ♀. In the Sarcopsyllids there is a similarly great reduction in the bristles of the abdomen as exists in those of the thorax. Two rows of bristles to each tergite of segments one to seven of the abdomen may be considered normal in *Siphonaptera*, though there are many species with more than two rows. These two rows are in the genus *Pulex* usually found at least on the first tergite, but the anterior row has disappeared in the ♀♀ of several allies of *Pulex irritans*, for instance in *P. pallidus*, as well as in both sexes of the species of *Malacopsylla*; the posterior row, however, is always well developed. Between each pair of long bristles of this row there is always a small hair in all *Pulicidae*. In the *Sarcopsyllidae* the anterior row of bristles is represented only on the first tergite, and only in the ♂♂. The second row is most complete in the ♂ of *Hectopsylla psittaci*, in which there are four or even five fairly long bristles on each side of the tergites one to seven; but this row differs from that of the *Pulicidae* in the small hairs in between the bristles being practically absent. From this row, which represents doubtless the ancestral type of abdominal vestiture of hairs in the Sarcopsyllids, to the

more reduced state of the bristles two lines of development can be traced. In the genus *Dermatophilus* the dorsal bristles have disappeared, only one bristle above the stigma remaining. In *Hectopsylla* and *Echidnophaga*, however, the most ventral bristles have been lost, the dorsal ones remaining. In the last two genera, with the exception of the ♂ of *Hectopsylla psittaci*, previously referred to, there are two bristles or only one, the first and the seventh tergites having often three bristles on each side. The lost bristles are often replaced by extremely minute hairs. The subdorsal bristle of the anterior tergites is rather stout in several species (as, for instance, in *C. gallinaceus*), being stouter than the bristles on the posterior segments. The bristles are placed usually on or near the middle of the segments; in some species, however, they have become shifted towards the base. While in *Echidnophaga* and *Dermatophilus* the tergites of segments one to seven bear each at least one bristle, the middle tergites of *Hectopsylla* have lost the bristles entirely.

Besides these bristles the seventh tergite bears in the *Siphonaptera* as a rule at least one long apical bristle standing usually on a cone, the bristle being rarely missing. This apical bristle with its two usual companions is placed in *Pulex* at a small distance from the apical edge of the segment, this edge not being emarginate, as is the case in those *Siphonaptera* in which these bristles are quite apical. Among the *Sarcopsyllidae* only the genus *Echidnophaga* has preserved a single apical bristle, which is present in both sexes, the bristle being sometimes much longer than the other bristles of the same segment, sometimes the same size, or smaller, according to the species.

The bristles on the abdominal sternites of the *Sarcopsyllidae* are always few in number, the proximal sternites being often devoid of bristles, though there are generally one or more extremely minute hairs present.

The swollen abdomen of the pregnant female of the *Sarcopsyllidae* is such a very conspicuous character in *Dermatophilus penetrans* that in the early history of the classification of *Siphonaptera* it has been advanced as the main distinction from the genus *Pulex*. We now know that the swollen abdomen of the ♀ is not confined to Sarcopsyllids, and that not all the Sarcopsyllid females become largely extended. In the swollen abdomen of pregnant ♀♀ of insects generally it can be noticed that the dorsal and ventral chitinated plates of each segment and the segments *inter se* have become separated, the connecting membranes being exposed to view. The last segment or segments and also the basal one are usually not extended or not to the same degree as the middle segments. This normally extended abdomen of the female is found in the family *Pulicidae* in a number of genera, such as *Malacopsylla*, *Vermipsylla*, and *Chaetopsylla*, the dorsal and ventral plates being more or less widely apart. As a matter of course the abdomen of the pregnant ♀ is in all *Siphonaptera* swollen to some extent, but the plates do not become separated except in the comparatively few species with sedentary habits. Now, in *Sarcopsyllidae* the swelling of the abdomen is different in each of the three genera into which we have divided the family. The swelling is

exhibited least in *Echidnophaga*. In this genus, judging from our material, the segmental plates of the pregnant ♀♀ are but little separated, the plates covering each other at least partly. The abdomen retains its general shape, the enlargement being in some of the species described below hardly equal to that found in *Pulex irritans*.

The female abdomen of *Hectopsylla* is quite different. The segmental plates are here placed widely apart when the abdomen is distended, the dorsal plates being quite separate from the ventral ones, the abdomen resembling in this respect that of the genera *Chaetopsylla*, *Malacopsylla*, and *Vermipsylla*. In the genus *Hectopsylla*, however, there is one very singular specialization, restricted to this genus, not being met with anywhere else among *Siphonaptera* as far as we know. The sternites of segments two to seven, which in other *Siphonaptera* consist each of a single plate, are in *Hectopsylla* completely divided in the middle line so that these segments bear three plates instead of two, all well apart from one another on the extended abdomen. This division of the ventral plate of the segments minimises the resistance of the plates. The swollen abdomen of a ♀ *Hectopsylla* has consequently quite a different aspect from that of a ♀ *Echidnophaga*, the connecting membranes being well exposed and the three brown plates of each segment (two to seven) being easily recognized on the white background. We mention incidentally that the abdominal sternites of the ♂♂ of *Hectopsylla* are *not* divided.

The swollen abdomen of *Dermatophilus* is again quite different from that of any other *Siphonapteron*. In this genus the abdomen becomes globular by swelling enormously in the central region. The three proximal segments are pushed forward, as

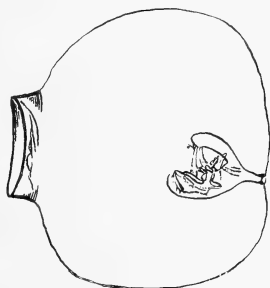


FIG. D

it were, and the other segments backwards, the membrane between the third and fourth segments being enlarged to a very great extent. In *D. caecata* the abdomen totally envelops the head and thorax as shewn in the accompanying diagram (Fig D).

Owing to the great diversity in the development of the legs of the *Sarco-*
psyllidae, both as regards the degree of specialization as well as the direction of

development, there is little in the legs by which to distinguish the present family as a whole from the other *Siphonaptera*. The mid coxa is very narrow in all the species of *Sarcopsyllidae*. The posterior portion of the hind coxa is reduced, becoming gradually narrower apically in *Hectopsylla* and *Echidnophaga* and being apically excised in *Dermatophilus*, the coxa, therefore, being widest near the base. The tibiae have usually no bristles on the lateral surfaces, or only one or two. The legs of the various species of Sarcopsyllids have no other characters in common. It is not possible, however, to mistake the leg of a Sarcopsyllid for that of any other Siphonapteron. Each genus has a sharply characterized type of leg not met with in genera other than *Echidnophaga*, *Dermatophilus*, and *Hectopsylla*, these genera differing in the legs not only from one another, but each from all the other *Siphonaptera*. The general trend of the development of the legs is again reduction, but rather reduction in width than in length. The legs become the more slender the more they are specialized, the number of segments composing the Sarcopsyllid leg remaining the same as in other *Siphonaptera*. The power of jumping is reduced, being entirely lost in the pregnant ♀♀ of *Dermatophilus* and probably in *Hectopsylla*. The bristles of the legs are in the most generalized type of a Sarcopsyllid similar to those of *Pulex irritans*, *pallidus*, *leporis*, etc., their number and width becoming less and less in the specialized forms. Some of the bristles are prolonged, which is suggestive of the long tarsal bristles of some members of the genus *Pulex*, for instance, *P. cleopatrae*.

The number of bristles on the forecoxa is never large, being largest in some *Echidnophaga* and smallest in *Hectopsylla*. There are some rather numerous but very short and stout bristles scattered over the surface of the forecoxa of *Dermatophilus penetrans* not found in the other two genera. Similar short bristles are situated also on the mid and hind coxae and the femora of *Dermatophilus penetrans*. These bristles are longer in the ♂ than in the ♀. The mid coxa is distinctly more ovate in *Dermatophilus* than in the other two genera. There are posteriorly at the apex of the mid and hind coxae either two bristles (as in some *Echidnophaga*) or only one.

The hind coxae of the genera are very different in shape and armature. In *Hectopsylla* they are simply truncate at the apex, bearing at the apical margin and near the anterior edge a number of bristles more or less arranged seriatly. In *Echidnophaga* the hind coxa (Pl. I, Fig. 7, 8) is apically produced into a truncate, strongly chitinized, process, and on the inner side of the coxa there is a patch of short spine-like bristles, such as are often met with among *Pulicidae*, the bristles being only more numerous in *Echidnophaga*. There is no trace of this patch in *Hectopsylla*. A similar, but less strongly chitinized process, is found in *Dermatophilus*, this genus lacking, however, like *Hectopsylla*, the patch of short bristles, and having the process more pointed than it is in *Echidnophaga*. On the other hand, there is a peculiar specialization in the trochanter and femur of the hind leg of *Hectopsylla*.

The trochanters of the *Siphonaptera* bear anteriorly a pair of bristles on or near the middle. These bristles are present in the *Sarcopsyllidae*, but have a more distal position than in other fleas. In *Hectopsylla* the groove in which these bristles are inserted on the posterior trochanter is enlarged and deepened, appearing as an excision in side-view; the upper edge of this groove projecting forward and downwards (Pl. I, Fig. 6). In a similar way, the pair of subbasal ventral bristles of the hind femur is situated in *Hectopsylla* in a deep groove, the portion of the femur in front of this groove forming a prominent hook (Pl. I, Fig. 6). Behind the groove the ventral edge of the femur is angulate, the angle corresponding to the small tooth found in several species of *Pulex* from the Old World (for instance, *Pulex cleopatrae*, *pallidus*, etc.) Those subbasal ventral bristles of the hind femur are preserved in *Hectopsylla* and *Echidnophaga*, but they are absent from *Dermatophilus*. The place where they are situated in those genera is also in *Dermatophilus* less chitinized than the rest of the femur.

The skeleton of all the femora is in *Echidnophaga*, and to a less degree also in *Dermatophilus*, internally incrassate just behind the subbasal membranaceous place, as is also the case in *Pulex*. As in many *Pulicidae* there is on the inner surface* of the hind femur of the *Sarcopsyllidae* a row of bristles. The number of bristles in this row is very much reduced in some species of *Echidnophaga*, there being only two or three bristles left in *Echidnophaga aethiops*. The hairs at the dorsal edge of the mid and hind femora vary much in number. The curved apical dorsal bristle of the femora is stout in *Echidnophaga*, but short and very weak in *Dermatophilus*, the species of the genus *Hectopsylla* being in this respect intermediate.

We have stated above that the tibiae are practically devoid of external bristles in all the species of *Sarcopsyllidae*, the row accompanying the dorsal bristles in other *Siphonaptera* being represented by one or two bristles only, or not at all. The dorsal bristles, however, do not present such a uniform development in the various species. We regard as the most generalized state of development in *Siphonaptera* a tibia with eight pairs of dorsal bristles placed in notches, including the apical bristles. One or the other of these pairs is usually reduced, the notch being obliterated or vestigial. The fifth pair and the apical pair are the most prominent, the third and the sixth are the first to be reduced or to disappear altogether, and after these the seventh pair. The same order is followed in the *Sarcopsyllidae*. In this family there are from three to seven pairs of dorsal bristles on the mid tibia, the lowest number being found in *Dermatophilus*. The proximal pair is always small, and the notch in which it is situated is practically obliterated; it is altogether lost in *Dermatophilus*, which retains the second, fifth, and the apical pairs. The notch of the third pair is also never developed in the *Sarcopsyllidae*, and the pair of bristles is, at the utmost, represented by a short but stout sublateral bristle and a minute hair.

* These bristles have been figured, by all authors we believe, as standing on the outer side of the femur.

The tarsi of the *Sarcopsyllidae* represents, like the tibiae, various degrees of development from a *Pulex*-like tarsus to the highly modified tarsus of *Dermatophilus*. There are no hairs on the ventral surface of the tarsal segments, except at the lateral edges. The proportional length of the segments varies to a certain extent, the fore and mid tarsi agreeing with those of *Pulex* and allied genera in the first segment being shorter than the second. The difference in length is, however, very slight in *Dermatophilus*, which has very slender tarsi. The most interesting differences between the various species are exhibited by the fifth segment and the claw.

In most *Siphonaptera* there is a smaller or larger number of minute hairs on the ventral surface of the fifth tarsal segment. These hairs are absent from all the *Sarcopsyllidae*. This negative character, however, is not confined to that family, there being only a few such hairs in *Pulex irritans*, *pallidus*, and allies, and none in *Lycopsylla* and *Malacopsylla*.

The fifth segment bears ventrally at the apical edge from 4 to 0 bristles in *Siphonaptera*. The highest number in the genus *Pulex* is three, one in the middle and one on each side of it, the lateral ones being usually somewhat proximal of the middle one. Of these three bristles a lateral one has disappeared in most species of *Pulex*, the other two either retaining their position towards each other or the proximal (or lateral) one moving distad so as to be on a level with the median one. In the *Sarcopsyllidae* we find never more than two bristles, which stand close together, the outer one being usually a little behind the other. This pair of apical bristles is present in most *Echidnophaga*, in which genus the bristles sometimes vary in size according to the species. They also occur in two of the three species of *Hectopsylla* and in *Dermatophilus penetrans* (the tarsi of *Dermatophilus caecata* are not known to us). In three species of *Echidnophaga* the outer bristle is lost, the median one alone remaining, while in *Hectopsylla pulex* both bristles have disappeared. Of the three *Echidnophaga* which possess one such bristle only two agree so closely with *E. gallinaceus* that their specific distinctness is not beyond doubt. This being so, it may be concluded that among a sufficiently large number of specimens of *E. gallinaceus* there will be found individuals with one such bristle only, at least on one of the tarsi. On the other hand, among the specimens of those species which have normally one bristle occasionally an individual will possibly be found with two bristles.

The lateral bristles of the fifth tarsal segment are in *Siphonaptera* very often of importance for the characterization of species, affording in many cases specific distinctions which are easily recognized. Near the apex of the segment there is always a thin hair on each side, placed on the dorsal surface of the segment. This subapical hair is usually long, but sometimes rather short. It is present in all the *Sarcopsyllidae*, with the exception of *Dermatophilus*. Between this hair and the base of the segment, but on the ventral side, there is in the *Pulicidae* a row of four, five, or six bristles, which are usually short and stout. The first bristle is often shifted towards the middle

of the ventral surface of the segment, being placed in many *Pulicidae* in between the second pair. In other species this first bristle is lost on each side. In others again, the fourth is replaced by a fine hair. These bristles are in several species of Sarcopsyllids much more reduced in size and number than in *Pulicidae* (Pl. III, Fig. 26; Pl. IV, Fig. 28.) In *Hectopsylla psittaci*, however, there are no less than eight bristles on each side, at least on the mid tarsus (Pl. IV, Fig. 32). In this species there is apparently an increase in the original number of lateral bristles, the increase having taken place in the apical region of the segment. None of the other species of *Sarcopsyllidae* have more than five bristles, the fifth always being much thinner than the others. The number is reduced to four and three in some species, the bristles being all very thin in *Dermatophilus*. The claw of *Siphonaptera* bears usually a basal ventral projection. This process is occasionally lost in the *Pulicidae*, for instance, in *Lycopsylla*. There is one species of *Echidnophaga* in which the claw has a large basal projection (Pl. III, Fig. 24); in other species of Sarcopsyllids the projection is very small, and in others again lost altogether (Pl. IV, Fig. 28). The gradation exhibited by the various Sarcopsyllids in respect to the claws is complete, *Dermatophilus* possessing the greatest specialization, the claw being in this genus very slender, like the whole tarsus.

The posterior abdominal segments which are partly modified for the purpose of copulation we now propose to discuss. It is well known that these segments are usually so diversely developed in the various species among insects that they afford very good diagnostic characters, more especially in the ♂♂. In *Siphonaptera* these characters are the more important for descriptive work as there are frequently but few other characters by which to distinguish the more closely allied species with any degree of certainty. Modification for sexual purposes is found in segments eight and nine of the ♂♂. In the ♀♀, however, it is the eighth segment and often also the seventh sternite which has assumed a peculiar shape. The eighth and ninth segments of the ♂♂ we propose to discuss first.

The tergite of the eighth segment bears in both sexes the last stigma which is usually situated in a more or less large hairy cavity, the tergite being often divided in the mesial line. On account of the development of the sensory plate on the ninth tergite the dorsal portion of the eighth tergite is in both sexes usually much shorter than the lateral portion. The relative size of the eighth tergite and sternite is very variable in the *Siphonaptera*. Originally the two plates were doubtless of nearly equal size, as is the case in the preceding segments. From this original state of organization development in two opposite directions has taken place. In some *Pulicidae* the eighth tergite of the ♂♂ has become reduced and the sternite enlarged, while in other *Pulicidae* the tergite is enlarged and the sternite reduced, the latter being sometimes represented only by a narrow strip of chitin or being occasionally vestigial. This small sternite occurs in a number of species of *Ceratophyllus*, while all the other *Siphonaptera* have a large or comparatively large eighth sternite. In some species of

Ceratophyllus the sternite is intermediate in size, while in others again it is large. The *Sarcopsyllidae* have the eighth sternite similar to that of *Pulex irritans* and its allies. The sternite is much longer ventrally than it is dorsally, and is therefore much arched ventrally. In one of the new *Sarcopsyllids* it is modified in a peculiar way, as is described in the body of this paper (Pl. II, Fig. 19). The large eighth sternite forms a kind of cover for the genitalia proper, protecting them ventrally and anally when the ♂ crawls beneath the ♀ and bends the abdomen upwards for the purpose of copulation. The enlargement of the eighth sternite and the curvature of its ventral surface can thus be readily understood. The great reduction of this sternite in so many species of *Ceratophyllus* is, however, difficult to explain from the utilitarian point of view. In *Hectopsylla* (Pl. II, Fig. 17 and 18) as well as *Dermatophilus* (Fig. F, p. 56) the eighth sternite of the ♂ is very deeply sinuate on each side.

The clasping organs are portions of the ninth segment. The tergite of this segment consists of three main portions, a dorsal part with the sensory plate upon it, to which we shall refer hereafter, and on each side a lateral part, called the clasper, bearing several appendages. These claspers are as a rule not separated

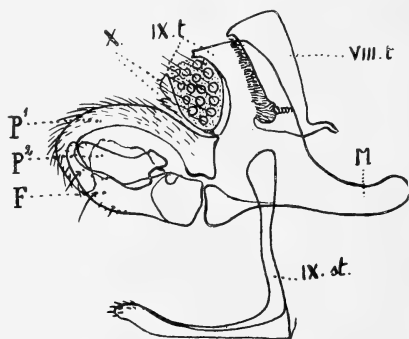


FIG. E

from the dorsal part of the tergite by a suture, but are continuous with it. However, in some instances (*Chaetopsylla*) there is a suture between the clasper and the dorsal portion of the tergite separating them almost entirely. The clasper with its appendages can be best understood we think by comparing it with that of *Pulex irritans*, which represents in our opinion a more generalized type than the clasper of the other *Pulicidae*. The ninth tergite (Fig. E) is proximally produced into a long process (M) acting as a lever or handle, the *manubrium*, as it is termed by WAGNER. Above this manubrium there is another process which is very small and belongs to the eighth tergite, which tergite is much reduced in *P. irritans*. This small process or manubrium of the eighth tergite is found only in *Pulex irritans* and *leporis*, and again among the *Sarcopsyllids* in the genus *Echidnophaga*, the process being absent from all the other

Siphonaptera. The clasper of *Pulex irritans* bears distally three separate processes, each being moveable by itself, there being a suture (or joint) between each process and the main body of the segment. The upper process (Fig. E, P¹) is broad in *P. irritans* and hairy. The second and third processes (P² and F) are much smaller, and form together a kind of claw reminding one of the pinchers of a lobster, the upper process (P²) being slightly curved downwards, and the lower process (F) upwards. The lower process is longer proximally than the upper, extending much further proximad.

These three processes, of which the two lower ones form a pair of pinchers, occur in a similar shape ONLY in *Pulex leporis* (= *goniocephalus*) among the *Pulicidae* and *Ceratopsyllidae*. The allies of *Pulex pallidus* (*cleopatrae*, *nubicus*, *isidis*, etc.) have also, three processes, but the two lower ones have completely lost their pincer-like appearance, while there are never three free processes in any other Pulicid or Ceratopsyllid. On the other hand, the processes of *Pulex irritans* and *leporis* are found again in the *Sarcopsyllidae*, the resemblance being very close indeed between these organs in *Pulex irritans* and in the species of *Echidnophaga* and *Hectopsylla*, as will be seen by comparing Fig. E. and Fig. 16-22. The genus *Dermatophilus* has also preserved the pair of pinchers, but the upper process of this pair is fused together with the main body of the clasper, there being no suture separating this process (Fig. F). The dorsal process (P¹) moreover, found in the other Sarcopsyllids as in *Pulex irritans*, has become completely lost. The state of development of the various portions of the claspers of *Dermatophilus* throws some light on the homology of the various parts of the clasper in those *Siphonaptera* which do not possess the three separate processes found in *Pulex irritans*. As there is doubtless a close phylogenetic connection between *Pulex irritans*, *pallidus*, etc., and the other genera of *Pulicidae*, it may be asked what has become of the three separate processes found presumably in the ancestral forms of those *Pulicidae* and the *Ceratopsyllidae* which have only one free process, the so-called 'Finger'? One point offers no difficulty whatever. A comparison of the claspers of the various *Siphonaptera* shows at once the homology of the lowest process (F) of *P. irritans* and the Sarcopsyllids with the 'Finger,' which is articulated to the clasper. The second process (P²) of *P. irritans* is in the other Pulicids merged together with the main body of the clasper, as in *Dermatophilus penetrans* (Fig. F), forming usually a more or less slender projection which has sometimes preserved an appearance similar to that found in *Pulex irritans*, for instance in some of the *Ceratopsyllidae*. The uppermost process (P¹) has either become completely lost, or it has become reduced and like the middle process merged together with the clasper. In *Ceratophyllus hilli* the articulation between the finger and the clasper has also disappeared (*Nov. Zool.* xi. t. 11. Fig. 43). In *Ctenocephalus canis* and *felis* the uppermost process is vestigial, the middle process has developed into a rather large flap, and the lowermost, though shortened, has preserved a shape resembling the same process of *P. irritans*.

Now, the great resemblance between the claspers of *P. irritans*, *leporis* and the Sarcopsyllids in contradistinction to the dissemblance between the claspers of *P. irritans* and those of the other *Pulicidae* is surely highly convincing evidence of the correctness of our contention that the Sarcopsyllids are closely related to *P. irritans*.

The clasper of the Sarcopsyllids offers some interesting specific and generic differences, the three genera *Dermatophilus*, *Hectopsylla*, and *Echidnophaga* having each distinctive features in this organ. The manubrium of the clasper is longitudinal in direction in *Dermatophilus* and *Echidnophaga* (Pl. II and III, Fig. 18-22), while it is vertical and very short in *Hectopsylla* (Pl. II, Fig. 16 and 17). The dorsal portion of the segment bearing the sensory plate is almost completely separated from the clasper in *Dermatophilus* and *Hectopsylla*. In *Echidnophaga* the segment is much wider in the dorsal line than above the manubrium (apart from the processes of the clasper), while in *Hectopsylla* the clasper is widened frontad, the small manubrium projecting downward from the lower anterior angle. There is in *Hectopsylla* a second small manubrium projecting upward from the upper corner of the dilated part. The processes vary much in size and shape in the different species (compare Pl. II and III).

The ninth sternite of the *Siphonaptera* has generally the shape of a boomerang in a lateral view, the internal arm being subvertical, extending from the clasper downward, and the external or ventral arm being more or less horizontal. The two 'boomerangs' of the two sides of the body are either entirely separate, or they are connected with one another at the angle, or the horizontal parts are completely united. In the *Sarcopsyllidae* the ninth sternite has this boomerang shape in *Echidnophaga*. In *Dermatophilus* the sternite is represented by a rather broad, elongate, horizontal plate on each side (Fig. F). The ventral portion of the sternite is also in *Hectopsylla* much wider than in *Echidnophaga*. The distal part of this ventral portion protrudes in *Hectopsylla* beyond the apex of the eighth sternite, forming a large flap which has the appearance of being articulated with the eighth segment (Pl. II, Fig. 17 and 18). Both in *Dermatophilus* and *Hectopsylla* the vertical portion of the ninth sternite is apparently represented by an internal incrustation on the eighth sternite.

In the ♀ it is the eighth segment (Pl. I and II, Fig. 9-15) which has undergone modifications for sexual purposes, and sometimes also the seventh sternite, the latter especially often in *Ceratophyllus* and *Ctenophthalmus*. The seventh sternite is simple in the Sarcopsyllids as it is in *Pulex irritans* and most other members of the genus *Pulex*. The tergite and sternite of the eighth segment were originally doubtless of nearly equal size, as in the preceding segments. In the *Sarcopsyllidae* as in many other *Siphonaptera* the tergite has become much enlarged, while the sternite is reduced to a very small plate. The tergite is in the *Sarcopsyllidae* completely divided in the mesial line.

The dorsal portion of the ninth tergite in *Siphonaptera* is practically identical in the two sexes. The sensory plate differs in *Hectopsylla* and *Dermatophilus* very essentially from that of *Echidnophaga*. The bristle-bearing grooves are separated in the

former two genera into a patch of eight grooves on each side, while *Echidnophaga* agrees with the *Pulicidae* in having a larger number of grooves (as many as thirteen or fourteen on each side). The anal (or tenth) segment is in so far of interest in the Sarcopsyllids as the stylet is missing in the ♀♀ of *Hectopsylla* and *Dermatophilus*, while it is present in *Echidnophaga*. The absence of the stylet is, however, not confined to those two genera of *Siphonaptera*, the genera *Lycopsylla* and *Chaetopsylla* among the *Pulicidae* being also without a stylet.

The number of stigmata is the same in the Sarcopsyllids as in other *Siphonaptera*, with the exception of *Dermatophilus*. In this genus the second and third segments of the abdomen have lost the stigmata in the female, doubtless in connexion with the peculiar mode of expansion referred to above. The stigmata or rather the cavities in which they are situated, are often different in the sexes of *Sarcopsyllidae*. The stigma of the eighth segment is always large. There is a peculiar difference in respect to this stigma between the three genera. In *Echidnophaga* the cavity of this stigma is hairy as in other *Siphonaptera*. In *Dermatophilus* the hairs are few in number, and in *Hectopsylla* there are no hairs in the cavity. The female has only one bursa copulatrix.

List of genera and species mentioned in the introduction :—

- Ceratophyllus* CURTIS, *Brit. Ent.* IX. no. 417 (1832).
Ceratophyllus charlottensis BAKER, *Journ. N. York Ent. Soc.* VI. p. 56 (1898).
Ceratophyllus hillii ROTHSCHILD, *Nov. Zool.* IX. p. 622. n. 15. t. 11. fig. 43, 44 (1904).
Chaetopsylla KOHAUT, *Allatt. Közlem.* II. p. 37 (1903).
Ctenocephalus canis CURTIS, *Brit. Ent.* III. no. 114. fig. A—E, and 8 (1826).
Ctenocephalus felis BOUCHÉ, *Nov. Act. Acad. Leop. Carol. Nat. Cur.* XVII. 1. p. 505 (1835).
Ctenophthalmus KOLENATI, *Paras. Chiropt.* p. 33 (1857).
Ctenophthalmus wernmanni ROTHSCHILD, *Nov. Zool.* IX. p. 642. n. 31 t. 14. fig. 75, 77, 79 (1904).
Ichtnopsylla WESTWOOD, *Intr. Classif. Ins., Synops. Gen.* p. 125 (1840).
Lycopsylla novus ROTHSCHILD, *l.c.* p. 602. n. 1. t. 7. fig. 1-4 (1904).
Malacopsylla WEYENBERGH, *Period. Zool.* III. p. 271 (1881).
Pulex australis ROTHSCHILD, *l.c.* IX. p. 613. n. 8. t. 9. 10. fig. 29, 34, 36 (1904).
Pulex buhlsi WAGNER, *Hor. Soc. Ent. Ross.* XXXV. p. 5 (1900).
Pulex cleopatrayae ROTHSCHILD, *Ent. Mo. Mag.* (2). XIV. p. 84. t. 1, 2. fig. 4, 8, 13, 17 (1903).
Pulex cleopontis id., *Nov. Zool.* IX. p. 614. n. 9. t. 10. fig. 32 (1904).
Pulex cocyii id., *l.c.* p. 617. n. 12. t. 9, 10. fig. 26, 31 (1904).
Pulex irritans LINNÉ, *Syst. Nat.* ed. X. p. 614. n. 1 (1758).
Pulex leporis CURTIS, *Brit. Ent.* IX. n. 417 (1832).
Pulex pallidus TASCHENBERG, *Die Flöhe* p. 65. t. 1. fig. 9 (1880).
Pulex nubicus ROTHSCHILD, *Ent. Mo. Mag.* (2). XIV. p. 84. t. 11. fig. 10, 16 (1903).
Pulex riggenbachii id., *Nov. Zool.* IX. p. 611. n. 7. t. 8, 9. fig. 19, 20, 24 (1904).
Pulex simonsi id., *l.c.* IX. p. 616. n. 11. t. 9, 10. fig. 30, 37 (1904).
Vermiphsylla SCHIMKEWITSCH, *Zool. Anz.* VIII. p. 75 (1885).

Family SARCOPSYLLIDAE

Sarcopsyllidae TASCHENBERG, *Die Flöhe* p. 43 (1880); BAKER, *Proc. U. S. Nat. Mus.* XXVII. p. 373 (1904).

Hectopsyllidae BAKER, *l.c.* (1904).

Rhynchoprionidae *id.*, *l.c.* XXIX. p. 124 (1905).

♂ ♀. Frons longer than occiput, bearing usually two moderately long hairs, the upper one standing in front of the eye; these hairs often reduced or even absent. Not more than nine bristles on each side of the occiput (2, 3, 4), usually less; no row of short hairs along the antennal groove. No genal comb, but the post-oral angle of the gena produced downwards into a more or less curved triangular lobe. Eye present, but the pigment reduced or absent in *Dermatophilus caecata*.

Antennal cavity open behind. Antenna the same in the sexes. The club segmented only on hinder side, bearing on this side a row of three hairs accompanied further downwards by a small fourth hair; these hairs often reduced in size and number or completely lost.

Mouth subterminal, the labrum and mandibles being directed obliquely forward. Labrum and mandibles broad, the latter heavily serrate. Maxilla triangular, obtuse or pointed. Maxillary palpus consisting of four segments, the first being as long as the second or longer. Rostrum very pale, almost transparent, being reduced in chitinization, but not in length; consisting of two or three segments, including the basal unpaired labium, there being only one joint in the labial palpus.

Thorax strongly reduced, the three tergites together shorter than the first abdominal tergite; each tergite bearing one row of bristles, variable in number and length, mostly very small, the most ventral one of the pro- and mesothorax being the longest; no combs. Pleural plate of prosternite usually produced posteriorly into a distinct obtuse conical lobe. Sternum and epimerum of mesosternite not separate, no internal incassation indicating the meral suture; hinder ventral edge of mesosternite produced into a lobe, which is variable in size. Episternum of metathorax large, bearing one small bristle, which is sometimes minute and often absent; epimerum large, vertical, or so widened as to reach to the third abdominal segment, one vertical row of not more than six bristles, occasionally with one or two bristles in front of the row.

One row of bristles on the abdominal tergites, containing on each side not more than five bristles, usually less, a second, anterior, row being vestigial in the ♂♂ on the first tergite; one apical bristle on seventh tergite in *Echidnophaga* separate from apical edge, this bristle absent from *Hectopsylla* and *Dermatophilus*.

Hind coxa widest near the base, produced into a truncate lobe anteriorly at the apex in *Echidnophaga* and *Dermatophilus*, while in *Hectopsylla* the posterior femur is produced anteriorly above the subbasal sinus.

Jumping power reduced or absent. Tibiae without bristles on the lateral surfaces, or only one or two. Hind femur on inner side with a row of four or more bristles, the number seldom reduced to two. Three to seven pairs of dorsal bristles on hind tibia. No hairs on the ventral surfaces of the tarsi, except at the sides; first segment shorter than second in fore and mid tarsi; fifth segment usually with two short bristles ventrally at the apex, standing close together, in some species one, in others none; three to eight lateral bristles on fifth segment. Claw with or without basal projection.

♂. Eight sternite large. Clasper with three processes, the second and third forming a kind of pincers, uppermost process absent in *Dermatophilus*. Ninth sternite 'boomerang'-shaped, or the internal, vertical, arm of the elbowed sternite vestigial or absent, the sternite separated in the mesial line, except at the proximal ventral angle.

♀. Seventh sternite simple. Eighth tergite large, sternite very small. Stylet absent or present. One bursa copulatrix. Ten stigmata, except in ♀ *Dermatophilus*, where the abdominal segments two and three have no stigma.

The early stages are known only of one species: *Dermatophilus penetrans* (see this species).

Key to the genera:—

- (a) Hind coxa with patch of spines on inner side, *Echidnophaga*.
 „ without such a patch of spines—*b*,
- (b) Hind femur with large basal tooth-like projection, *Hectopsylla*.
 „ simple, *Dermatophilus*.

I. Genus ECHIDNOPHAGA

Sarcopsyllus WESTWOOD (non *Sarcopsylla* id., 1840), *Ent. Mo. Mag.* XI. p. 246 (1875).

Sarcopsylla, TASCHENBERG, *Die Flöhe* p. 5 (1880) (partim).

Echidnophaga OLLIFF, *Proc. Linn. Soc. N.S. Wales* (2). I. p. 172 (1886) (type: *E. ambulans*).

Argopsylla ENDERLEIN, *Deutsche Tiefsee—Exp.* III. 7. p. 263 (1903) (type: *Sarcopsyllus gallinaceus* WESTWOOD).

Xestopsylla BAKER, *Proc. U. S. Nat. Mus.* XXVII. p. 374 (1904) (type: *Sarcopsyllus gallinaceus* WESTWOOD).

♂ ♀. Frons angulate; a horseshoe-shaped transverse depression behind the angle. An internal incensation of the skeleton from the base of the antennal groove upwards to the mesial line of the head. Two bristles on the frons, with a minute hair in between, the upper bristle in front of the eye. Occiput reduced in length. Eye more or less widely separate from the antennal groove. Posterior genal process long, separating more or less completely the prosternite from the antennal groove. Labium and labial palpus mostly not separated by a joint (suture).

Second antennal segment with several long bristles on the apical projection. Non-segmented side of club of antenna with a row of usually three hairs accompanied by one minute hair further frontad.

Mesosternite produced posteriorly into a small obtuse lobe. No hair on either the episternum or the sternum of the metathorax; epimerum vertical, very much higher than long.

Abdominal segments not, or very little, separate in swollen ♀♀. Tergites of both sexes with at least one bristle, which is subdorsal, seventh tergite with an apical bristle. Sensory plate of ninth abdominal tergite with thirteen or fourteen grooves on each side. Last stigma hairy. Posterior (= meral) portion of hind coxa gradually becoming narrower apically; apex of hind coxa anteriorly produced downwards into a prominent truncate lobe; a patch of numerous short spine-like bristles on inner side of hind coxa. Trochanter and femur of hind leg simple; a pair of hairs at the subbasal sinus of the hind femur. Curved apical bristle of femora rather stout.

♂. Eighth abdominal tergite with a short manubrium. Manubrium of clasper longitudinal in direction; ninth tergite wider dorsally than above manubrium; clasper not separate from dorsal portion of segment by a suture; three free processes on clasper, the two lower ones forming a pair of pincers. Ninth sternite 'boomerang'-shaped, not or only a little projecting beyond the eighth segment.

♀. Stylet present. Abdominal sternites not divided in the mesial line.

Though OLLIFF's description, if taken verbally, does not apply to any species of *Siphonaptera* known to us, we have no doubt that the species called by him *ambulans*, l.c., belongs into the present genus of *Sarcopsyllidae*. The description gives one the impression of being incorrect. The antenna is stated to be four-jointed; the mandible is said to be serrate only in the apical half, the tibiae are described as having 'rather large spines on the external margin,' etc. Such statements are certainly not correct, and we may, therefore, consider it also an error of observation that the labial palpus is described as three-jointed. On the other hand, OLLIFF mentions some important points which appear to us to be of more weight than the above statements quoted from the description. The specimens of *Echidnophaga ambulans*—OLLIFF had evidently only ♀♀, though he does not mention to which sex his specimens belonged—were so firmly attached to the host by the rostrum as to render their removal a matter of considerable difficulty. They did not appear to possess the power of jumping. Their body is said to be almost destitute of bristles except at the anus, and the claws of the tarsi to be simple. Taking now further into consideration that some of the species of the present genus are common parasites in Australia on various hosts, including *Echidna hystrix*, we are fairly bound to conclude that *Echidnophaga ambulans* is congeneric with WESTWOOD's *Sarcopsyllus gallinaceus*; unfortunately *Echidnophaga* is the first generic term for this genus, WESTWOOD's *Sarcopsyllus* being a misspelling for *Sarcopsylla* proposed more than thirty years earlier for the South

American Chigoe or Jigger. But the term *Echidnophaga* cannot be rejected on account of its being an inappropriate name; the majority of generic names are more or less inappropriate, if the original (= philological) meaning of the word is considered.

Although, however, *Echidnophaga* is in our opinion an earlier term for the same genus which BAKER named *Xestopsylla* in 1904, and ENDERLEIN *Argopsylla* in 1903, we do not know which of the Australian species of this genus is the one which OLLIFF named *ambulans*. We have applied the name to a species of which we have received a large quantity of ♀♀, besides one ♂, from Paramatta, near Sydney, but whether this assumption is correct can only be decided by a careful examination of the type of *ambulans*.

There are eight species of *Echidnophaga* known to us. The genus does not occur in America, apart from *E. gallinaceus* which has been introduced with the host. The larva is not known of any of the species.

The species occur on mammals and birds. They are not confined each to one kind of host.

Key to the species :—

- (a) Claw of tarsus with a very large basal projection—*E. macronychia*.
 " " " small " —*b*.
- (b) Fifth tarsal segment on each side with one heavy subbasal bristle, a thinner medium one, and a small postmedian hair—*E. liopus*.
 Fifth tarsal segment on each side with five heavy bristles—*E. bradyta*.
 Fifth tarsal segment on each side with three heavy bristles and a smaller fourth—*c*.
- (c) Fifth tarsal segment with two apical ventral bristles—*d*.
 " " " " one " " bristle—*e*.
- (d) Second bristle of fifth tarsal segment midway between first and third—*E. gallinaceus*.
 Second bristle nearer the first than the third—*E. larina*.
- (e) Occiput of ♀ with lateral lobe—*E. ambulans*.
 " " without " —*f*.
- (f) Second segment of maxillary palpus longer than the third—*E. murina*.
 " " " " not longer than the third—*E. aethiops*.

1. *Echidnophaga macronychia*, spec. nov.

(Pl. I, Fig. 7, 8; Pl. II, Fig. 15; Pl. III, Fig. 22, 24).

Head.—The frons is strongly rounded at the centre, being slightly angulate. The oral edge is feebly convex in the middle; measured from the ventral frontal corner to the apex of the ventral genal process it is shorter than the genal edge measured from the base of that process to the apex of the posterior genal process.

The ventral genal process is slightly curved backwards. The occiput is in the dorsal line two-thirds the length of the frons. Its hinder edge is somewhat convex in the middle. There is only one long bristle on the occiput standing near the hinder edge above the antennal groove. The mandibles reach nearly to the middle of the four femur. They are rather slender, being only a little wider near the base than the maxillary palpi. The latter reach almost to the apex of the anterior coxa, the last segment being as long as the distance from the eye to the ventral frontal corner of the head. The proportional lengths of the segments are 18, 19, 14, 27, the proportions varying a little. The club of the antenna is globular in the ♀, being somewhat conical in the ♂.

Thorax.—The pronotum bears one long stout bristle ventrally close to the pleural plate, and a vertical row of six thin hairs in the ♂ and four or five in the ♀. The pleural plate of the prothorax is ventrally as long as the distance between the eye and the ventral frontal corner of the head. The mesonotum has only one long bristle near the ventral edge and a few small hairs in the dorsal half. There is one long bristle on the mesothoracic sternite. The metanotum and metasternum do not bear bristles. The epimerum of the metathorax has a row of four bristles, which are nearly equidistant from one another, the upper two being closer together than the second and third.

Abdomen.—The tergites one to six bear dorsally on each side a long but very slender bristle, there being an additional bristle in front of it on the first tergite. The seventh tergite has a rather long and stout bristle near the apex, standing on a short cone. In front of this bristle there are two thin hairs on each side. The sternites of segments two to six bear no bristles. On the seventh sternite there is one bristle, besides some very small hairs. The stigmata have about the same diameter as the groove of insertion of the subapical bristle of the seventh tergite.

Legs.—The hind coxa bears on the inner side a patch of from eighteen to twenty-four spine-like bristles. There is one bristle posteriorly near the apex of the hind coxa (Pl. I, Figs. 7, 8). The hind femur bears a lateral row of from six to nine bristles. The dorsal bristles of the tibiae are rather stout. The mid and hind tibiae bear six dorsal incisions, the apical one included. The longest bristle of the fifth dorsal pair of bristles of the hind tibia is less than twice as long as the tibia is broad at the apex, the longest apical dorsal bristle not reaching to the apex of the first hind tarsal segment. The second mid tarsal segment is half as long again as the first. The first hind tarsal segment is more than half the length of the hind tibia, and bears in the ♂ two or three and in the ♀ three or four bristles on each side, besides the apical ones.

The fifth segment (Pl. III, Fig. 24) of all tarsi has five heavy bristles on each side, besides a subapical hair. The claw is stout, being curved in the middle, and bearing a prominent basal projection. The measurements of the mid and hind tarsi are as follows :—

	First Segment	Second Segment	Third Segment	Fourth Segment	Fifth Segment
Mid tarsus, ♂ - -	7	10	7	5	18
„ ♀ - -	9	14	9	6	18
Hind tarsus, ♂ - -	26	17	10	8	18
„ ♀ - -	33	21	11	8	18

Modified Segments.—♂. The upper process of the clasper (Pl. III, Fig. 22) bears two long bristles ventrally near the apex, and a shorter one at one-third before the apex. The third process (F) is about two-thirds the length of the manubrium (M). The narrow proximal portion of this process is half the length of the free distal portion. The internal, vertical, portion of the ninth sternite (Pl. III, Fig. 22, ix *st.*) has about the same width as the external, horizontal portion, both being equally slender.

♀. The eighth tergite bears a row of short stout bristles before the apex, and some longer ones further proximally (Pl. II, Fig. 15). The bristles vary somewhat in number. The stylet is one-third longer than it is broad, bearing at the apex one long bristle accompanied by a short slender one.

Length: ♂, 1.3 mm.; ♀, 1.8 mm.

We have a series of specimens from West Australia, collected by Mr. C. J. TUNNEY, as follows:—

- 1 ♂. From Kojonup, off Bettongia lesueuri. 12th March, 1904.
 12 ♀ ♀. From Kojonup, off Bettongia lesueuri. 12th March, 1904.

2. *Echidnophaga bradyta*, spec. nov.

(Pl. II, Fig. 13, 19; Pl. III, Fig. 23)

A very dark coloured species.

Head.—The frons is subangulate or rounded in the ♂, and obtusely angulate in the middle in the ♀. The ventral genal process is curved backwards. The oral edge from the apex of this process to the ventral corner of the frons is as long as the genal edge measured from the base of that process to the apex of the posterior genal process. The occiput, which is in the dorsal line two-thirds the length of the frons, bears one long bristle near the apex above the antennal groove, there being another rather long one obliquely above this bristle, and several minute hairs on the side and back of the occiput. The hind margin of the occiput is in the ♀ dilated at or below the middle into a more or less prominent lobe. The mandibles are near the base much broader than the palpi. The last segment of the latter is longer than the first, the proportional lengths of the segments being in the ♂ 15 to 19, 18 to 22, 15 to 16,

28 to 29; and in the ♀, 19 to 23, 19 to 22, 12 to 14, 25 to 27. The club of the antenna is in both sexes a little longer than it is broad.

Thorax.—The pronotum bears a row of five or six bristles, the lower one alone being long. On the mesonotum there is one long bristle near the ventral edge, and a row of four or five shorter ones which are placed further dorsad. The very short metanotum has no prominent bristles, but there are two or three extremely small hairs upon it. On the epimerum of the metathorax there are two rather thin bristles below the stigma, one of which is sometimes missing, and nearer the ventral edge one long one, and in some examples two.

Abdomen.—The tergites one to six bear on each side two bristles, besides some very minute hairs, the seventh tergite having three bristles instead of two. The subapical bristle of the seventh tergite is rather thin and short. The sternites of segments 2 to 6 have in the ♀ each one bristle besides some very small hairs standing in a more or less regular vertical series, in the ♂ only some minute hairs being present. The stigmatal cavities of the ♀ are enlarged, their diameter being more than twice the diameter of the groove of insertion of the subapical bristles of the seventh tergite. In the ♂ the abdominal stigmata are very much smaller than the three thoracal ones.*

Legs.—The number of spine-like bristles on the hind coxa varies from thirty to forty-two. There are two bristles on the mid and hind coxae posteriorly above the apical lobe. The hind femur bears a row of nine to twelve bristles. The mid and hind tibiae bear six dorsal incisions, the apical one included. The dorsal bristles of the fore tibia are short and stout. One bristle of the second, fourth, and apical pairs of the hind tibia is long, the middle one being about twice as long as the tibia is broad at the apex. The first hind tarsal segment is a little over half the length of the hind tibia; it bears on the hinder side four or five bristles, and on the anterior side two or three, exclusive of the apical ones. The longest apical bristle of the second hind tarsal segment does not quite reach to the apex of the fifth segment. This latter segment bears on each side five stout bristles, besides a subapical hair, the ventral apical bristles being also stout (Pl. III, Fig. 23). The claw has a distinct basal projection. The measurements of the mid and hind tarsi are as follows:—

	First Segment	Second Segment	Third Segment	Fourth Segment	Fifth Segment
Mid tarsus, ♂ - -	13	17	10	8	23
„ ♀ - -	18	20	12	9	27
Hind tarsus, ♂ - -	36	23	15	10	26
„ ♀ - -	41	25	16	11	30

* The stigma situated on the metathoracal epimerum is here counted as a thoracal one.

Modified Segments.—♂. These segments are very different from those of the other species of *Echidnophaga*. The eighth sternite is very large and is apically produced into an acute process (Pl. II, Fig. 19, viii. st). The internal part of the ninth tergite is long (ix. t). The manubrium (M) is widened at the apex. The hairy process (P¹) of the clasper is very large, gradually widening towards the apex, which is rounded. This process is about as long as the head, measured from the ventral frontal corner to the apex of the posterior (horizontal) genal process. The second process of the clasper (P²) is peculiar, being produced dorsally into a tooth. The finger (F) is long and slender. The ninth sternite (ix. st) is distally dilated into a rather broad lobe.

♀. The apex of the eighth tergite (Pl. II, Fig. 13) is bisinuate. It bears a row of short stout bristles on the outer side and a similar row of thinner ones on the inner side. There are on the outer side also some bristles at the ventral edge and a variable number on the lateral surface. The stylet (sty) is less than twice as long as it is broad. It is cylindrical and bears one long bristle and two short ones.

Length:—♂, 2.1 mm.; ♀, 2.3 mm.

Our specimens are collected by Mr. C. H. B. GRANT. We have—

4 ♂♂, 30 ♀♀.	From Deelfontein, Cape Colony, off <i>Suricata tetradactyla</i> .	April and June, 1902.
1 ♂, 1 ♀	" " " <i>Xerus capensis</i> .	April, 1902.
1 ♀	" " " <i>Zorilla striata</i> .	August, 1902.

3. *Echidnophaga larina*, spec. nov.

(Pl. I, Fig. 12; Pl. II, Fig. 18; Pl. III, Fig. 25)

Head.—The frons is angulate in both sexes at one-third the way from the ventral frontal corner to the antennal groove, the angle being emphasized in the ♀ by the frons being more deeply impressed than in the ♂ just behind the angle, the latter therefore projecting usually as an acute tubercle. The bristles on the head are all short, except the eye-bristle and the bristle which is situated near the oral edge. The small hairs on the back of the frontal part of the head are longer than is usually the case in this genus. The ventral genal protection is not curved backwards. The edge of the occiput is simple in both sexes. The occiput is in the dorsal line half the length of the frons. The mandibles are very broad, being near the base in the ♂ more than twice, and in the ♀ about four times the width of the maxillary palpi. The first segment of the latter is a little longer than the last, especially in the ♀, the proportional lengths of segments being 20 to 24, 16 to 19, 11 to 14, 18 to 21.

Tborax.—The pronotum bears four small bristles on each side, the ventral one being the longest, the mesonotum has two still smaller ones, and the metanotum one or two minute ones on the back. The metanotum is dorsally longer than the mesonotum. The apical projection of the prosternite is very short and obtuse. The

mesosternite bears two bristles. The metathoracical epimerum has three or four bristles from the stigma downwards, the bristles being equidistant.

Abdomen.—The tergites bear on each side one bristle, which stands near the base of the segment, the first and the seventh segments alone possessing two bristles. There is a small subapical bristle on the seventh tergite. The sternites are bare of bristles, but there are a few very minute hairs on them. The stigmatal cavities of the ♀ are large, being only a little smaller than the stigmatal cavity of the metathoracical epimerum. In the ♂ the diameter of the abdominal stigmatal cavities is about one-fourth smaller than that of the epimeral cavity.

Legs.—The hind coxa bears a patch of about thirty to forty spine-like bristles. The hind femur has a row of six or seven bristles. The hind tibia have three deep dorsal incisions from the base beyond the middle, besides a vestige of a subbasal incision. Between the third incision and the apical bristles there is generally one small hair. The longer bristle of the pair standing in the third incision is slender and rather short, not being much longer than the tibia is broad at the apex. The first hind tarsal segment is half the length of the hind tibia measured along the anterior edge. This segment bears one or two lateral bristles besides the apical ones. The longest bristle of the second hind tarsal segment reaches beyond the middle of the fifth. The fifth segment which is long and slender, bears on each side three rather long spines and a fourth short one, besides the ordinary subapical hair (Pl. III, Fig. 25). The first and second spines stand closer together than the second and third. The two ventral apical spines are very stout. The claw is slender. Its basal projection is vestigial. The measurements of the mid and hind tarsi are as follows :—

	First Segment	Second Segment	Third Segment	Fourth Segment	Fifth Segment
Mid tarsus, ♂ ...	14	15	11	10	27
„ „ ♀ ...	18	19	12	10	32
Hind tarsus, ♂ ...	30	19	12	11	30
„ „ ♂ ...	38	23	16	11	35

Modified Segments.—♂. The eighth sternite is widest below. The manubrium (M) is broad, the apex being ventrally rounded. The hairy process (P¹) of the clasper (Pl. II, Fig. 18) is of nearly even width throughout, being elbowed proximally of middle. The second process (P²) is angulate ventrally before the apex. The finger (F) is, beyond the middle, abruptly curved upwards. The ventral horizontal portion of the ninth sternite (ix. st.) is slightly curved upwards, being produced at the apex into a short hook which points downwards.

♀. The eight tergite (Pl. I, Fig. 12) is rather broadly sinuate at the apex. It bears about six bristles on the outside, arranged in a halfring, and a row of five or six on the inner side. The stylet (sty) is not quite twice as long as it is broad. It is cylindrical and bears three bristles at the apex, one being long and the others short.

Length :—♂, 1·7 mm. ; ♀, 2·6 mm.

5 ♂	♂, 69 ♀	♀. From Deelfontein, Cape Colony, off <i>Orycteropus capensis</i> .	July, 1902	(C. H. B. Grant)
1 ♂	"	" " " "	"	<i>Erinaceus frontalis</i> , "
5 ♀	♀	" " " "	"	<i>Hystrix cristatus</i> . July, 1902 "
1 ♂	"	" " " "	"	<i>Herpestes pulverulentus</i> . Nov., 1902 "
1 ♀	"	Somaliland	26 Feb., 1900	(Erlanger and Neu-
4 ♀	♀	Daroli, Abyssinia	"	<i>Canis familiaris</i> . 20 Jan., 1901 (Erlanger) [mann
1 ♀	"	" " "	"	<i>Hyaena crocuta</i> . 18 Feb., 1901 "
	"	" " "	"	<i>Felis leopardus</i> . 18 Feb., 1901 "

4. *Echidnophaga aethiops*, spec. nov.

We have only one ♀ of this species, which is allied to, but perfectly distinct from, *E. gallinaceus*.

Head.—The frons is not angulate, the head being almost evenly and very feebly rounded from the hinder edge to the mouth. The occiput is dorsally less than half the length of the frons. There are two long bristles above the antennal groove on the occiput. The oral edge measured from the ventral frontal corner of the head to the apex of the ventral genal process is longer than the genal edge measured from the base of this process to the apex of the posterior (horizontal) genal process. The mandibles are shorter and narrower than in *E. gallinaceus*. The maxillary palpus is quite different, the first segment being a little shorter than the last, and the second being hardly more than half the length of the fourth, not being longer than the third. The hinder edge of the occiput does *not* bear a lateral lobe.

Thorax.—The metathoracic episternum bears an irregular series of five or six bristles, and has in addition a small bristle in front of the stigma.

Abdomen.—The bristles of the proximal tergites are less strongly chitinized than in *E. gallinaceus* ♀. There is a row of six bristles on the seventh tergite on the two sides together, the dorsal bristles being small. The subapical bristle of this segment stands much closer to the edge than in *gallinaceus*. The stigmatal cavities are much smaller than in the ♀ of that species, their diameter being about half the length or that of the stigmatal cavity of the metathoracic epimerum.

Legs.—The hind coxa bears a patch of about sixteen spine-like bristles, besides some longer hairs. There are only two bristles on the hind femur instead of a row. The fifth tarsal segment is shorter than in *E. gallinaceus*, and the basal projection of the claw more distinct. The measurements of the mid and hind tarsi are as follows :—

		First Segment	Second Segment	Third Segment	Fourth Segment	Fifth Segment
Mid tarsus	8	9	7	6	14
Hind tarsus	18	12	8	7	16

Modified Segments.—The eighth sternite is less deeply sinuate ventrally at the apex than in *E. gallinaceus*, there being also a few more bristles in the present species.

Length : ♀, 1.7 mm.

We have one ♀, collected by Mr. C. H. B. Grant at Klipfontein, Namaqualand, off a bat.

5. *Echidnophaga gallinaceus*

(Pl. I, Fig. 1; Pl. II, Fig. 14; Pl. III, Fig. 21; Pl. IV, Fig. 27)

Sarcopsyllus gallinaceus WESTWOOD, *Ent. Mo. Mag.* XI. p. 246 (1875) (Ceylon, off Chicken);

RITSEMA, *Versl. Tijdschr. Ent.* XIX. p. 76 (1876) (*S. gall.* probably a *Hectopsylla*).

Sarcopsylla gallinacea, TASCHENBERG, *Die Flöhe* p. 55. n. 2. t. i. fig. 5-5a (1880).

PACKARD, *Insect Life* VII. p. 23. fig. 3, ♀ (1894); HARTZ. *ibid.* p. 280 (1894) (on horses).

WAGNER, *Hor. Soc. Ent. Ross.* XXVIII. p. 440. fig. 1, 2 (1894).

BAKER, *Canad. Ent.* XXVII. p. 20 (1895).

OSBORN, *Div. Ent. Dept. Agric. Bull.* V. p. 144. fig. 76, 77 (1896).

BLANCH., *Bull. Soc. Nat. Acclim. France* XLIV. p. 210. fig. ♂, ♀ (1897).

ENDERL., *Zool. Jahrb.* XIV. 1. *Abth. Syst.* p. 552. t. 34. fig. 6 (1901).

Pulex spec. JOHNSON, *Proc. Ent. Soc. Washingt.* I. p. 59 (1890).

Pulex pullulorum id., *i.e.* I. p. 203 (1890) (habits).

Argopsylla gallinacea ENDERLEIN, *Deutsche Tiefsee—Exp.* iii. 7. p. 263. fig. 6 (1903).

Xestopsylla gallinacea, BAKER, *Proc. U.S. Nat. Mus.* XXVIII. p. 375, 434 (1904).

Although both sexes of this species have several times been figured, some of the essential distinguishing characters have been overlooked. The following short description of both sexes supplements these deficiencies to some extent :—

Head.—The frons is strongly angulate in the ♀ before the middle, and rotundate-angulate in the ♂ (Pl. I, Fig. 1, ♀). The occiput is short, measuring dorsally one-half or less of the frons. There are two long bristles above the antennal groove, the anterior one standing behind the base of the antennal groove, and the posterior one near the hinder edge of the occiput. This hinder edge is in the ♀ produced laterally in the middle into a rounded lobe (Pl. I, Fig. 1). The mandibles are more than twice the width of the maxillary palpus near the base. The first segment of the maxillary palpus is as long as the last in the ♂, and longer than the last in the ♀. The ventral genal process is slightly curved backwards. The first segment of the club of the antenna is large, oblique in position, covering the greater part of the next three segments.

Thorax.—The pro- and mesonotum have each a row of bristles, the lower ones being long. The metathoracal epimerum bears a row of four to six bristles.

Abdomen.—The tergites one to seven bear on each side one bristle, the bristle being heavier on the anterior than on the posterior segments. On the first and seventh there are in the ♂ two bristles on each side, the first tergite bearing, moreover, an additional bristle in front of them. On the seventh tergite there is, besides, a subapical bristle (Pl. III, Fig. 21). The stigmatal cavities of the abdomen are in the ♀ nearly the same size as that of the metathoracal epimerum. In the ♂ they are much smaller.

Legs.—The hindfemur bears a row of four to six bristles. The fifth tarsal segment has on each side four bristles, besides a subapical hair, the fourth bristle being much smaller than the others (Pl. IV, Fig. 27). There are two subapical ventral bristles on this segment. The claw has a slight basal projection. The measurements of the mid and hind tarsi are as follows :—

		First Segment	Second Segment	Third Segment	Fourth Segment	Fifth Segment
Mid tarsus, ♂	5-7	7-9	6-7	5	15-16
Mid tarsus, ♀	8-9	10	7	6	16
Hind tarsus, ♂	17-21	11-13	7-8	6-7	15-17
Hind tarsus, ♀	20-23	13-14	9	7	18

Modified Segments.—♂. The eighth sternite is obliquely emarginate apically, becoming gradually shorter dorsally. The internal portion of the ninth tergite is much shorter than it is wide, being longest dorsally. The manubrium (Pl. III, Fig. 21, M) is long and very slender. The hairy flap (P') of the clasper bears one long hair ventrally at the apex. The free distal portion of the finger (F) is much longer than the narrowed proximal portion. The ninth sternite (ix. st.) is very slender.

♀. The eighth tergite (Pl. II, Fig. 14) is sinuate ventrally at the apex. It bears on the outer side a few slender bristles, and on the inner side a curved row of five to six short ones, of which latter the upper three are strongly chitinized. The stylet is very short, being only a little longer than it is broad.

This species occurs in the tropical and subtropical districts of Asia, in the Ethiopian region, and in the southern districts of the Nearctic region, being, doubtless, distributed by the introduction of the domestic fowl. We have not yet received it from Central and South America.

WESTWOOD's specimens of *gallinaceus* are apparently not contained in the Hopeian department of the Oxford Museum, there being no specimens of this species among the Siphonaptera of that institute, which Professor E. B. POULTON kindly

allowed us to examine. As we possess the species here described from Central Asia, the Fiji Islands, from various parts of Africa (West, South, and East), and from the Malagasic subregion, we are probably right in applying the name *gallinaceus* to this insect.

- 5 ♂ ♂, 5 ♀ ♀. From Russian Armenia, off *Erinaceus auritus*. (Collected by Zugmayer).
 1 ♂. „ Anan, Transcaspia, off *Erinaceus auritus*. (Received from Dr. Wagner).
 1 ♂. „ ? off *Felis rubiginosa*.
 7 ♂ ♂, 5 ♀ ♀. „ Namosi, Fiji, off domestic *Gallus gallus*. (Miss Embleton and K. J. Cameron)
 12 ♂ ♂, 45 ♀ ♀. „ Deelfontein, Cape Colony, off *Suricata tetradactyla*. April, 1902.
 (C. H. B. Grant).
 2 ♂ ♂, 5 ♀ ♀. „ Deelfontein, Cape Colony, off *Herpestes badius*. (C. H. B. Grant)
 1 ♂. „ Durban, off a hawk. 15 October, 1904. (H. W. Bell-Marley).
 100 ♀ ♀. „ Gold Coast, off domestic *Gallus gallus*.
 2 ♂ ♂, 2 ♀ ♀. „ Wakkerstroom, off domestic cat. July, 1904. (C. H. B. Grant).
 2 ♂ ♂, 2 ♀ ♀. „ „ off „ dog. July, 1904. (C. H. B. Grant).
 2 ♂ ♂, 5 ♀ ♀. „ St. Maurice, Madagascar, off *Hapalemur griseus*. (Dr. Tuschebaud).
 2 ♀ ♀. „ Port Nolloth, Namaqualand, off *Lepus capensis*. (C. H. B. Grant).
 1 ♀. „ Berber, off *Lepus mesomelas*. 19 May, 1900. (Erlanger and Neumann).
 1 ♀. „ Daroli, N.E. Africa, off *Herpestes albicauda*. 25 January, 1901. (Erlanger).
 2 ♀ ♀. „ San Diego, Texas, off domestic fowl. December, 1894. (Mr. Toumey).
 2 ♀ ♀. „ Orangeburg, South Carolina, off horses. November, 1894. (G. T. Hartzell).

6. *Echidnophaga ambulans*

Echidnophaga ambulans OLLIFF, *Proc. Linn. Soc. N. S. Wales* (2). I. p. 172 (1886) (N. S. WALES, on *Echidna hystrix*); BAKER, *Proc. U. S. Nat. Mus.* XXVII. p. 431, 439 (1904); *id.*, *l.c.* XXIX. p. 124 (1905).

Sarcopsylla myrmecobii WATERHOUSE, *Proc. Ent. Soc. Lond.* p. 23 (1887) (*nom. nud.*, West Australia, off *Myrmecobius*).

OLLIFF's description of *ambulans* is as follows:—

‘Broadly ovate, castaneous, shining, with indistinct green reflections. Antennae capitate, finely setose. Eyes rather prominent, small, pale castaneous. Head moderately convex above, finely and indistinctly crenulate in front. Thorax short. Abdomen ovate, rather strongly convex above, somewhat truncate posteriorly; the anal region armed with a few strong bristles. Legs pale castaneous, tips of femora and tibiae darker; tibiae with two feeble notches on the external margins. Length, 2 mm.; greatest width, $1\frac{1}{3}$ mm.’

From this very general description it is impossible to decide which of the Australian *Sarcopsyllidae* is the insect from which the description was taken. As OLLIFF had numerous specimens—apparently all ♀♀—we applied to the Australian Museum for the loan of a specimen, but were informed that our request could not be complied with, the type of *ambulans* being unique.

We have two species of *Sarcopsyllids* to which the generic and specific descriptions of *Echidnophaga ambulans* apply equally well. We accept the name

ambulans for one of these two insects, though it is quite possible that the true *ambulans* is distinct from both. As OLLIFF's species was discovered in New South Wales we identify as *ambulans* that species of which we have received a large number of specimens from the same country. This is, of course, a mere surmise.

This *ambulans* does not differ from *E. gallinaceus*, except in one character. All the specimens of *ambulans* have on the fifth tarsal segment one apical ventral bristle only, instead of the two found in all the specimens of *gallinaceus* which we have examined. It appears to us probable that *ambulans* and *gallinaceus* are geographical forms of the same species. There may exist, probably in the Malay Archipelago, a form in which that differential character is either individually variable, or in which the fifth tarsal segment bears two such bristles on the fore and mid tarsi, and one only on the hind tarsus (or *vice versa*).

OLLIFF's specimens were taken off *Echidna hystrix*. We have :—

1 ♂, 94 ♀♀.	From Paramatta, near Sydney, off <i>Trichosurus vulpecula</i> .	April, 1904.	(Th. Schrader).
8 ♀♀.	„ Victoria, „ „ „		
1 ♀.	„ Kojonup, West Australia, off <i>Bettongia lesueuri</i> .	March, 1904.	(C. J. Tunney).
1 ♀.	„ Herdman's Lake, Perth, West Australia, <i>Diemenia superciliosa</i> (!)		(Dr. Woodward).
2 ♀♀.	„ Cranbrook, West Australia, off <i>Myrmecobius fasciatus</i> .	March, 1900.	(C. J. Tunney).
10 ♀♀.	„ Magitup, West Australia, off <i>Paragale lagotis</i> .	June, 1900.	(C. J. Tunney).

The occurrence on the Brown Snake (*Diemenia superciliosa*) is of interest, this being the first instance recorded of a flea occurring on a reptile.

7. *Echidnophaga murina*

Sarcopsylla gallinacea, TIRABOSCHI, *Bull. Soc. Zool. Ital.* XI, p. 172 (1902) (Italy on *Mus alexandrinus*); *id.*, *Arch. Parasitol.* VII. p. 124 (1903) (Italy); *id.*, *Lc.* VIII. p. 303. fig. 42 ♀ (1904).

Sarcopsylla gallinaceus var. *murina* *id.*, *Lc.* VII. p. 124 (1903) (Italy).

Sarcopsylla gallinacea var. *italica* *id.*, *Lc.* (Italy).

Sarcopsylla rhynchopsylla *id.*, *Lc.* VIII. p. 309. fig. 46 (1904) (Italy, on rats).

Argopsylla rhynchopsylla, BAKER, *Proc. U. S. Nat. Mus.* XXIX. p. 125 (1905).

This is the only species of *Sarcopsyllidae* hitherto recorded from Europe.

DR. TIRABOSCHI, when redescribing the insect as a species in 1904 under a third new name, had some doubts as to its being distinct. Through the kindness of HERR KOHAUT, of Budapest, who lent us the two specimens which he had received from DR. TIRABOSCHI, we have been able to compare this insect with the allied species. We find it to be a very close ally of *E. gallinaceus*, but consider it distinct from that species on account of the differences mentioned hereafter.

Only the ♀ is known.

Head.—The head is a little longer than that of *E. gallinaceus*. The occiput bears two rather heavy bristles above the antennal groove, as in *E. gallinaceus*. The

hinder edge of the occiput is *not* produced into a distinct lobe as in that species, the lobe being vestigial. The maxilla is a little slenderer than in *E. gallinaceus*.

Thorax.—The pro- and mesothorax bear each two long bristles, and further upwards two more small ones. The epimerum of the metathorax has a row of four bristles, there being in one specimen one additional bristle in front of the stigma.

Abdomen.—The tergites bear one bristle on each side, the seventh tergite possessing an additional bristle near the apex. The stigmatical cavities are rather larger than in *E. gallinaceus*. There is apparently no bristle on the seventh sternite.

Legs.—The hind femur, which bears a row of bristles in most specimens of *E. gallinaceus*, has on the inner side one or two bristles near the base and another near the apex. The tarsi, with the exception of one midtarsus, are absent in two specimens we have seen, the claw of which is, however, also broken off. The fifth segment of this midtarsus resembles that of *E. gallinaceus*, but the fourth lateral bristle is a little heavier, and there is only one apical ventral bristle, as is the case in *E. ambulans*.

Modified Segments.—The eighth tergite and the stylet are essentially as in *E. gallinaceus*.

Dr. TIRABOSCHI described this insect from specimens caught on rats in *Italy*. The specimens are most frequently found on the head of the host.

8. *Echidnophaga liopus*, spec. nov.

(Pl. I, Fig. 2; Pl. III, Figs. 20, 26)

Head.—The small hairs on the back of the head are heavier than in *E. gallinaceus*. The frons is more strongly angulate than usually, being more depressed behind the angle, the angle bearing at each side a small tooth which points upwards (Pl. I, Fig. 2). The ventral genal process is longer than in *E. gallinaceus*, the oral edge being, however, shorter than the genal edge measured from the base of that process to the apex of the horizontal genal process. The occiput measured dorsally is about two-thirds the length of the frons. It bears one bristle above the antennal groove, generally accompanied by a small hair. The hinder edge of the occiput is dilated laterally in the middle, the lobe being very short and broad. The second segment of the maxillary palpus is nearly as long as the fourth, being proportionally longer than in *E. gallinaceus*.

Thorax.—The pro- and mesothorax bear each four bristles on each side, while there are two or three bristles on the metathoracal epimerum.

Abdomen.—The tergites two to six have one bristle on each side. The first and the seventh tergites, however, possess two. There is, moreover, on the seventh tergite a bristle between the middle and the apex of the segment. These bristles are slenderer than in *E. gallinaceus*. The seventh sternite bears one bristle on each side.

Legs.—There is one short stout bristle posteriorly at the apex of the mid and hind coxae. The thin hair usually accompanying these is, however, absent in thie

species. The hind femur has a lateral row of five or six bristles and bears at the dorsal edge eight to ten fine hairs. The tarsal segments are longer than in *E. gallinaceus*, this being especially marked in the fourth segments. The second segment of the fore tarsus is nearly twice as long as it is broad, the fourth segment being only a little longer than it is broad. The second segment of the mid tarsus is more than twice as long as it is broad, being somewhat longer than the tibia is broad at the apex. The fourth hind tarsal segment is about twice as long as it is broad. The fifth segment of all the tarsi is quite different from that of every other species, being long and rather slender (Pl. III, Fig. 26). It bears on each side only one heavy bristle placed near the base. In one mid tarsus of one of our specimens there is a second bristle situated at the basal third on one side only. Between the middle and the apex of this tarsal segment there are two fine hairs, and at the apex a long thin hair. On the ventral side, at the apex of the segment, there is a pair of rather stout bristles. The claw is long and slender, being a little more curved than in *E. gallinaceus*. The measurements of the mid and hind tarsi are as follows:—

		First Segment	Second Segment	Third Segment	Fourth Segment	Fifth Segment
Mid tarsus, ♂ ♀	...	11	13	9	8	20
Hind tarsus, ♂ ♀	...	25	15	11	9	20

Modified Segments.—♂. The oblique distal edge of the eighth sternite is emarginate. The manubrium of the clasper is slenderer than in *E. gallinaceus*, and more curved. The long flap of the clasper is broader than in that species bearing three bristles at the ventral edge (Pl. III, Fig. 20, P¹). The third process of the clasper (F) is rather less curved than in *E. gallinaceus*.

♀. The eighth tergite is sinuate. It bears on the outer side two bristles beneath the sinus and a row of four above it, the uppermost bristle being short. On the inner side there is a row of three bristles, with some minute hairs in addition, most of these hairs being placed between the most ventral bristle and the one next to it. The stylet is about three times as long as it is broad, being bottle-shaped. The anal tergite bears a pair of heavy bristles which are about half as long again as the stylet.

Length: ♂, 1.4 mm., ♀, 1.8 mm.

We have a long series of both sexes from Mt. Anderson, West Australia, taken off *Ecbidna aculeata* by C. J. TUNNEY in November 1901. The species occurs also in India, where Captain WINDSOR found some ♀♀ on rats at Agra in February 1904.

2. Genus. HECTOPSYLLA

Hectopsylla FRAUENFELD, *Sitz. Ber. K. Ak. Wiss. Wien, Math. Nat. Cl.* XL. p. 462 (1860),

Rhynchopsyllus HALLER, *Archiv. Naturg.* XLVI. p. 72 (1880) (type: *pulex*).

Rhynchopsylla, TASCHENBERG, *Die Flöhe* p. 56 (1880).

♂, ♀. Frons rounded or angulate; no hoeshoe-shaped depression behind the angle. No internal incassation of the skeleton from the base of the antennal groove upwards to the mesial line of the head, but a dorsal incassation between frontal oral corner and antennal groove. Two bristles on the frons, with a minute hair in between; the upper bristle placed a little higher than in *Echidnophaga*, the lower bristle often minute. Hinder edge of occiput strongly slanting.

Eye well separate from the antennal groove. Posterior genal process long, separating the prosternite more or less completely from the antennal groove.

Second segment of the antenna with one long and several short bristles on the obtuse apical projection. No hairs on non-segmented side of club of antenna; club a little longer than in the other two genera.

Labium and labial palpi separated by a joint (suture).

Mandible of ♂ slenderer than that of ♀; serration less far extended basad.

Mesosternite produced posteriorly into a rather prominent obtuse lobe. One small bristle on metathoracic sternum, and a still smaller one on the episternum, epimerum vertical, very much higher than long.

Abdominal segments well separated in swollen ♀♀. Middle tergites without bristles either in both sexes, or in the ♀ only; the other tergites with at least one subdorsal bristle; no apical bristle on the seventh tergite. Sensory plate of ninth tergite with a patch of eight grooves on each side (Pl. I, Fig. 9, 10, 11).

Bristles on fore coxa few in number. Posterior (= meral) portion of hind coxa gradually becoming narrower apically. Hind coxa truncate at apex; no patch of spines on the inner side; no bristle on the posterior apical lobe. Trochanter and femur of hind leg (Pl. I, Fig. 6) each produced anteriorly into a tooth; the tooth of the femur large. A pair of hairs at the subbasal sinus of the hind femur. Last abdominal stigma not hairy.

♂. Eighth abdominal tergite without manubrium, the sternite very large, deeply sinuate (Pl. II, Fig. 16, 17). Clasper widened frontally, being wider than the dorsal portion of the ninth tergite, which is situated behind the sensory plate; a small manubrium (M²) projecting downwards from the ventral anterior angle of the dilated part, there being a second small manubrium (M¹) at the dorsal angle projecting upward; clasper almost completely separated by a suture from the dorsal portion of the segment; three free processes on clasper, the second and third forming a pair of pincers. Ninth sternite 'boomerang'-shaped; the ventral, longitudinal, portion projecting beyond the eighth sternite, wider than in *Echidnophaga*, consisting of several lobes; the internal vertical portion reduced.

♀. Without stylet; abdominal sternites completely divided in the mesial line, each consisting of two separate plates.

The genus is purely American. Only four species are known, all from South America. One of them (*H. psittaci*) occasionally infests the aviaries in Europe, being introduced by some South American birds.

Key to the species :—

- (a) Maxilla long, narrow, pointed, curved backwards—*H. pulex*.
Maxilla widest beyond middle, curved forward—*b*.
- (b) Fifth tarsal segment with eight bristles on each side, besides the subapical hair; epimerum of metathorax without process—*H. psittaci*.
Fifth tarsal segment with six bristles or less on each side, metathoracical epimerum of ♀ with curved process behind stigma—*c*.
- (c) Fifth tarsal segment with three or four bristles on each side; metathoracical epimerum with two bristles—*H. coniger*.
Fifth tarsal segment with six bristles on each side (♀; ♂ not known); metathoracical epimerum usually with three bristles—*H. broscus*.

1. *Hectopsylla coniger*, spec. nov.

(Pl. I, Fig. 5, 9; Pl. II, Fig. 16; Pl. IV, Fig. 30)

♂, ♀. This species, of which we have both sexes, can be easily recognized by the curved process of the metathoracical epimerum of the ♀, the sexual organs of the ♂, the fifth tarsal segment of both sexes, and by some characteristic details of other organs.

Head.—The frons is strongly angulate in the ♀, the angle being obtuse but not rounded; in the ♂ the angle is very strongly rounded off. The occiput bears in the ♀ a lateral apical lobe (Pl. I, Fig. 5). The end segment of the maxillary palpus is longer than in *H. psittaci*, the proportional lengths of the segments being in the ♂ 8, $5\frac{1}{2}$, $4\frac{1}{2}$, and 10, and in the ♀ 11, 8, $5\frac{1}{2}$, and $10\frac{1}{2}$. The bristles on the head are essentially the same as in *H. psittaci*.

Thorax.—The pronotum bears four bristles on each side. There is one long bristle on the mesonotum placed near the sternite, and some short hairs situated further dorsad. The metanotum does not bear any bristles in the ♀. The episternum of the metathorax is in both sexes produced into a triangular process. In the ♀ the epimerum of the metathorax bears also a process situated behind the stigma. This process is curved downwards. There are two long bristles on the metathoracic epimerum in both sexes.

Abdomen.—The ♂ has on each side two or three bristles on the first tergite, one or two on the second, one each on tergites 4 to 6, and one or two on the seventh tergite. In the ♀ the first, second, and seventh tergites bear each one hair near the base on each side, while the other tergites have no bristles.

Legs.—The bristles on the legs are fewer in number than in *H. psittaci*. The fore femur is devoid of bristles on the lateral surfaces. The hind femur, which is shorter than in *H. psittaci*, bears a series of five or six bristles in the ♂, and four or five in the ♀. The long bristle of the third dorsal pair of the hind tibia reaches to the apex of the tibia, while the longest apical bristle of this tibia reaches to the apex of the third tarsal segment. The first mid tarsal segment is distinctly shorter than the second. The fifth segment of all tarsi is proportionally much longer than in *psittaci*, this segment being in the hind tarsus of *coniger* as long as the first segment. The number of bristles of this segment is characteristic for *coniger*. There are in the ♂ on each side four bristles, on one mid tarsus only three, beside the long subapical hair, while there are always three bristles in the ♀. The claw is very slender, and shows a slight indication of a basal projection (Pl. IV, Fig. 30). The measurements of the mid and hind tarsi are as follows :—

		First Segment	Second Segment	Third Segment	Fourth Segment	Fifth Segment
Mid tarsus, ♂	...	7	10	7	6	19
Hind tarsus, ♂	...	19	12	9	8	19

The hind tarsus is missing in all our ♀♀.

Modified Segments.—♂. The plate of the clasper which bears the dorsal and the ventral manubrium is vertically longer than that of *H. psittaci* (Pl. II, Fig. 16). The large hairy flap of the clasper (P') has the ventral edge emarginate, the ventral apical angle being produced downwards. There are only two bristles on the clasper near the base of this process. The second and third lobe of the ninth sternite (IX st.) are broader than in *H. psittaci*.

♀. The eighth tergite bears externally a row of seven bristles (Pl. I, Fig. 9), while there are two series of bristles on the inner surface, the proximal row ending ventrally in a patch of very small hairs. The bristles on the anal segment are fewer in number than in *psittaci*.

Length : ♂, 1.3 mm. ; ♀, 2.3 mm.

We have one ♂ and fourteen ♀♀ from Pampa Olliga, Bolivia, a place situated at 3,000 m. altitude, 67° w., and 19° s. The late Mr. P. O. SIMONS found the specimens on *Conepatus arequipae*, 19 October 1901.

2. *Hectopsylla broscus*, spec. nov.

(Pl. IV, Fig. 29)

♀. This species is similar to *H. coniger*, but is easily distinguished from it by the following characters .—

Head.—The angle of the frons is strongly rounded. The bristles of the head are longer than in *coniger*. The two genal processes are longer and narrower. The second segment of the maxillary palpus is much shorter than the fourth segment, the proportion being 7 : 11 in *brosicus*, and 8 : 10 in *coniger*.

Thorax.—The processes of pro- and metasternite are narrower. The meta-thoracic epimerum bears usually three long bristles, rarely four or two.

Legs.—There is a lateral bristle on each side of the fore femur. The hind femur bears a series of eight or nine bristles. The tarsi are longer than in *coniger*, especially the fifth segment. This segment bears on each side six bristles, besides the long sub-apical pair, and has ventrally at the apex two short thin hairs (Pl. IV, Fig. 29).

Modified Segments.—The eighth tergite is broadly but shallowly emarginate apically, and bears a few more bristles than in *coniger*. Near the ventral edge of the segment there are three or four additional bristles standing separate from the vertical row of bristles. Proximally of these additional bristles (which are not present in *coniger*) there are several minute hairs.

We have a series of twelve ♀♀ of this species from Pampa Central, Argentina, found on *Conepatus humboldti*, by the late Dr. CARLOS BERG.

3. *Hectopsylla psittaci*

(Pl. I, Fig. 3, 6, 11; Pl. II, Fig. 17; Pl. IV, Fig. 32)

Hectopsylla psittaci FRAUENFELD, Sitz. Ber. K. Ak. Wiss. Wien, Math. Nat. Cl. XL. p. 462 (1860 (off a Parrot, Chile).

BAKER, Proc. U.S. Nat. Mus. XXVII. p. 375 (1904) ('Ceylon,' error; *psittaci* = *pulex*, error).

Pulex (*Hectopsylla* ?) *testudo* WEYENBERGH, Periodico Zoologico III. p. 267 (1879) (Argentina, off *Strix perlatata*).

Rhynchopsylla pulex, TASCHENBERG, Die Flöhe p. 56 (1880) (partim; *pulex* = *psittaci*, ex errore).

Our best thanks are due to Prof. Dr. O. TASCHENBERG, of Halle, Dr. HANDLIRSCH, of Vienna, Dr. STECK, of Bern, Dr. DUTOIT, of Bern, and Prof. Dr. DOERING, of Cordoba, for enabling us to compare typical specimens of *psittaci*, *testudo*, and *pulex*. The result of this comparison is different from what we expected it to be. While *testudo* is the same as *psittaci*, the *Rhynchopsyllus pulex* of Haller, is quite a different insect, though TASCHENBERG, l.c., had pronounced it to be identical with *psittaci*. However, the bad state of preservation of FRAUENFELD's specimens goes far to excuse that error.

As we have a good series of ♀♀ of both *psittaci* (= *testudo*) and *pulex*, and possess also the ♂ of *psittaci*, which has not yet been described, we take the opportunity of supplementing and correcting in this paper the original descriptions.

Head.—The frons of *psittaci* (Pl. I, Fig. 3) is longer in the ♀ than in the ♂, being longer than the occiput measured above the eye. It is rotundate-angulate at one-third the way from the mouth to the antennal groove. There is one rather long

bristle in front of the eye, and further forward two shorter ones. From the eye upwards there is a number of very short but distinct hairs arranged in three or four irregular longitudinal rows. The occiput bears three bristles above the antennal groove, the anterior one being smaller than the others, there are also several other hairs on the side, and a subapical row of five or six bristles. The proportional lengths of the four segments of the maxillary palpus are in the ♂ 11, 7, 6, and 10, and in the ♀ 19, 9, 6, and 10. The maxilla is short and slightly curved forward, being very different from the long and acute maxilla of *H. pulex*.

Thorax.—The pronotum bears a row of seven to ten bristles in the ♂, and of six to eight in the ♀. The sternite of the prothorax is posteriorly produced into a conical projection. The meso- and metanotum are larger in the ♂ than in the ♀. The mesonotum bears in the ♂ a row of five to seven bristles, while there are in the ♀ only two or three bristles standing on the lower portion of the notum. The metanotum has in both sexes a short row of bristles dorsally, the number of bristles being four to five in the ♂, and two or three in the ♀. There is one long bristle each on the meso- and metasternum near the upper edge. The metathoracal epimerum bears four or five bristles, one or two standing just beneath the stigma, and three more being placed in a vertical row a little more forward. The epimerum is rounded above, becoming narrowed ventrally.

Abdomen.—The tergites one to seven bear in the ♂ a row of four bristles on each side; in the ♀ there are three or four bristles only on the first and second segments, the third to six tergites being devoid of bristles, and the seventh bearing only one on each side. There are no bristles on the sternites of segments two to seven.

Legs.—The mid and hind coxae are wider at the apex than the trochanters, the anterior apical corner projecting a little. The posterior apical lobe of these coxae is rather long. It does not bear a bristle itself, but there is a long one just above it (Pl. I, Fig. 6) posteriorly. The hind femur bears a row of seven or eight bristles. There are no hairs on the lateral and ventral surfaces of the tibiae. The dorsal incisions are five in number, inclusive of the apical one. The dorsal bristles of the fore tibia are short and stout, except a bristle each of the third and apical pairs. All the bristles of the mid and hind tibiae are slender, the long middle one and the apical ones of the hind tibia being nearly as long as the tibia. The tarsal segments 1 to 4 have bristles only at the apex, these bristles being very long on the hind tarsus, the longest bristle of the second segment reaching nearly to the apex of the claw; sometimes there is a pair of bristles on the hinder side of the first segment beyond the middle. The fifth segments of the fore and mid tarsi are characteristic (Pl. IV, Fig. 32). It bears on each side a row of eight short stout bristles, besides a long sub-apical hair. There are also two spine-like bristles ventrally at the apex. The claw is very long and slender, but has a distinct basal projection. The measurements of the mid and hind tarsi are as follows:—

	First Segment	Second Segment	Third Segment	Fourth Segment	Fifth Segment
Mid tarsus, ♂ ♀ ...	11	11	7	6	16
Hind tarsus, ♂ ♀ ...	28	18	11	10	19

Modified Segments.—♂. The eighth tergite is small, while the sternite is very much enlarged. The sternite is peculiar in shape, bearing a very narrow and deep sinus as shown in the figure (Pl. II, Fig. 17). The proximal edge of the clasper between the ventral manubrium (M²) and the dorsal manubrium (M¹) is rounded. The edges of the large flap P¹ are practically straight. Close to the juncture of the finger (F) with the clasper there are three bristles. The external portion of the ninth sternite consists of three lobes, as shown in the figure (Pl. II, Fig. 17).

♀. The eighth tergite is very large, the sternite being very much reduced. This tergite (Pl. I, Fig. 11) bears a row of bristles near the apical edge, the edge being shallowly sinuate. There are also bristles on the inner side of the segment, these bristles being short and very numerous near the ventral apical corner. The anal segment bears behind the pygidial plate on each side ten or twelve long bristles, besides some short ones.

Length: ♂, 1.4 mm.; ♀, 1.8 mm.

We have:—

- 2 ♀ ♀. Received from the Vienna Museum, cotypes of *psittaci*.
 5 ♂ ♂, 120 ♀ ♀. „ „ „ Aviary in the Zool. Gardens in London, off various birds.
 October 1903. (E. OCKENDEN).
 27 ♀ ♀. „ „ „ Aviary of a Zoological Garden in Holland. Received from Prof.
 Dr. O. TASCHENBERG.
 10 ♀ ♀. „ „ La Plata, off *Columba livia*. Received from Dr. CARLOS BERG.

4. *Hectopsylla pulex*

(Pl. I, Fig. 4, 10; Pl. IV, Fig. 31)

Rhynchopsyllus pulex HALLER, *Archiv f. Naturg.* XLVI. p. 82. t. 4 (1880) (Brazil; off *Molossus* spec.).

Rhynchopsylla pulex, TASCHENBERG, *Die Flöhe* p. 57. t. 1. fig. 6, 6a, 7 (1880) (partim).

Hectopsylla psittaci, BAKER (non Frauenfeld, 1860), *Proc. U.S. Nat. Mus.* XXVII. p. 375. 434 (1904) (partim; 'Ceylon' error loci).

The ♂ of this species is not known. We have a series of ♀♀ which agree exactly with a typical specimen of *H. pulex*, received from Dr. DUROI, the son-in-law of the late Dr. HALLER.

Head.—The frons and occiput are evenly rounded together (Pl. I, Fig. 4). There is no trace of an angle on the frons. The occiput bears three bristles above

the antennal groove, there being three more short bristles further upwards, between the second bristle and the dorsal edge of the head. The strongly curved first segment of the maxillary palpus is much longer than the second and also than the fourth, the third being about half the length of the first. The proportions are : 11, 9, 5, $8\frac{1}{2}$. The maxilla is very different from that of the other species, being long and pointed, with the narrow apical half slightly curved backwards, as shown in the figure (Pl. I, Fig. 4, *max.*).

Thorax.—The pronotum bears a row of four bristles on each side, the most ventral bristle being the longest. The interspace between this ventral bristle and the next is wide, and there is an extremely minute hair halfway between these two bristles. On the mesonotum there is one long bristle, the episternum bearing also a bristle. The metanotum has a few small hairs on the back, while there is one minute hair on the episternum of the metathorax, and a bristle on the sternum. The metathoracical epimerum bears from four to six bristles. The prosternum is produced backwards into a rather long process, while the mesosternum and the metathoracical episternum are produced into a short blunt process.

Abdomen.—The first and second tergites bear each a row of four to six bristles near the base on the two sides taken together. Tergites 3 to 6 have no bristles, tergite 7, however, bears one small hair near the base. The sternites have no bristles. The stigmatal cavities of the abdomen are larger than that of the metathoracical epimerum.

Legs.—The hind coxa is longer than in *H. psittaci*. The hind femur has a row of four or five bristles on the inner side. The tibiae are essentially as in *H. psittaci*, the tarsi being, however, different. In the fore tarsus the first and second segments are about twice as long as they are broad, the third segment is half as long again as it is broad, and the fourth one-third longer than it is broad. The third segments of the mid and hind tarsi are also much longer than in *H. psittaci*. The fifth segment of all the tarsi is again slenderer than in *H. psittaci*, bearing on each side five bristles, and a long hair (Pl. IV, Fig. 31). There are no ventral apical bristles on this segment as there are in *H. psittaci*. The claw is very slender and nearly straight, bearing a very small basal projection, which is not nearly so prominent as in *H. psittaci*. The measurements of the mid and hind tarsi are as follows :—

	First Segment	Second Segment	Third Segment	Fourth Segment	Fifth Segment
Mid tarsus	14	12	11	7	16
Hind tarsus	27	18	15	11	20

Modifera Segments.—The eighth tergite (Pl. I, Fig. 10) bears on the outer side a row of about seven bristles. On the inner side, however, there is a row of about a dozen bristles, of which six or seven are long. In front of this row there is another more irregular row of short bristles. The number of bristles on this segment is much smaller than in *H. psittaci*.

Length: ♀ (extended), 2.7 mm.

HALLER's specimens were taken off a bat (*Molossus* = *Nyctinomus*) from Brazil. We have ten ♀♀ of this insect from Parana, Brazil, off *Histiotus velatus*, and another ♀ from Buenos Aires, off *Nyctinomus brasiliensis*, this last collected by the late Dr. CARLOS BERG.

In addition to these we have examined two of Dr. HALLER's specimens.

3. Genus. DERMATOPHILUS

Pulex LINNÉ, *Syst. Nat.* ed. X. p. 614 (1758) (partim; type: *irritans*).

Dermatophilus GUÉRIN, *Icon. Règne Anim., Ins.* p. 12 (1838 or 1839) (type: *penetrans*); LABOULB., *Bull. Soc. Ent. France* p. 155 (1874) (*Rhynchopriion* Herm. = *Argas*, a tick; *Dermatophilus* has priority over *Sarcopsylla*); *id.*, *l.c.* p. 114 (1875) (contra WESTWOOD).

Dermatophylus, LUCAS, in Guérin, *Dict. Pitt. Hist. Nat.* VIII. p. 394 (1839).

Sarcophaga WESTWOOD (Guild mss.; non Meigen, 1826), *Trans. Ent. Soc. Lond.* II. p. 200, 202 (1840).

Sarcopsylla id., *l.c.* p. 202 (1840) (type: *penetrans*); TASCHENB., *Die Flöhe* p. 44 (1880) (partim); BAKER, *Proc. U. S. Nat. Mus.* XXVII p. 374 (1904).

Rhynchopriion, KARSTEN (non HERMANN, 1804), *Bull. Soc. Impér. Moscou.* p. 72 (1864); GUYON, *Rev. Mag. Zool.* p. 64 (1866); BAKER, *l.c.* XXIX. p. 125 (1905).

Several authors have applied the term *Rhynchopriion* OKEN to this genus. In this they were wrong. HERMANN proposed that name for a tick in 1804.* OKEN, in his *Lebrb. Naturg.* iii. p. 402 (1815), employed the same name for his second and third genera of ticks. The *Pulex penetrans* (OKEN does not write *Rhynchopriion penetrans*) was merely put in between the second and third genus, because OKEN believed it to belong somewhere among the ticks.

As regards the names *Sarcopsylla* and *Dermatophilus* we think there can be no doubt that *Sarcopsylla* was published later than *Dermatophilus*. WESTWOOD, in 1865 (*Proc. Ent. Soc. Lond.* (3). ii. p. 91), claims priority for his name, while in 1874 and 1875 LABOULBÉNE (*Bull. Soc. Ent. France* p. 155, resp. 114) maintains that *Dermatophilus* was published before *Sarcopsylla*.

The facts, as far as we have been able to ascertain them, are these:—

Sarcopsylla was published in 1840. The name *Dermatophilus* appears first in the text of GUÉRIN's *Icon. Règne Animal*. The exact date of publication of this text is not known to us. WESTWOOD quoted the name *Dermatophilus* from this text at the end of his paper; but he says in *Intr. Class. Ins.* p. 493 (1840), that he had received

* Mém. Aptères. 1804.

advance sheets from GUÉRIN. We do not know if these sheets were really mere advance sheets, or whether GUÉRIN has published the text of the *Iconographie* in instalments as he did with the plates. However that may be, priority of publication for *Dermatophilus* is established by the fact that the name is dealt with in 1839 by LUCAS in Guérin, *Dict. Pitt. Hist. Nat.* VIII. p. 394, LUCAS spelling the name *Dermatophylus*.

There are two species of *Dermatophilus*, which present the following generic characters :—

♂, ♀. Frons angulate, the angle prominent and rather close to the frontal oral corner ; a horseshoe-shaped depression behind the angle. No internal incrassation of the skeleton from the base of the antennal groove upwards to the mesial line of the head. Antennal groove closed behind by the prosternite. The two frontal bristles found in the preceding genera much reduced or absent. Occipital bristles minute. Eye situated at the antennal groove, or at a short distance from it. Second antennal segment with one or several long but thin bristles on the apical projection. Club of antenna on non-segmented side with a row of from two to four hairs, or without hairs.

Thoracical tergites very short, the occiput almost touching the abdomen. Mesosternite produced posteriorly into a small obtuse lobe, the corresponding lobe of the prosternite vestigial. One minute hair on the metathoracic sternum, no hair on the episternum ; epimerum very large, reaching to the third abdominal segment.

Abdominal tergites one to seven with one bristle, which is lateral, standing above the stigma ; abdomen of pregnant ♀♀ globular, membrane between third and fourth segment enormously extended, the three proximal segments pushed forward, the other segments backwards. Sensory plate of ninth tergite with a patch of eight grooves on each side.

Mid coxa ovate. Posterior (= meral) portion of hind coxa excised apically ; apex of hind coxa anteriorly produced downwards into a prominent lobe. Trochanter and femur of hind leg simple. No hairs at the vestigial subbasal sinus of the hind femur ; curved apical bristle of femora weak. Tarsi very slender, bristles very long and thin ; first segment of mid tarsus very little shorter than second. Claw very slender, without basal projection.

♂. Eighth abdominal tergite without manubrium ; eighth sternite very large, divided on each side by a very deep and narrow sinus as in *Hectopsylla*. Manubrium of clasper longitudinal in direction. Clasper almost completely separated from the dorsal portion of the segment ; two processes, forming a pair of pincers, the upper one not separated from the clasper, the third (uppermost) process of the other Sarcopsyllids completely lost. Ninth sternite broad, internal vertical portion vestigial.

♀. Stylet absent. Segments two and three of abdomen without stigmata. Pregnant ♀ within the skin of the host.

The genus is American, *D. penetrans* having spread into the Aethiopian region.

The two species can be separated as follows :—

Eye distinct ; head and thorax of pregnant ♀ outside the abdomen—*D. penetrans*.

Eye vestigial ; head and thorax of pregnant ♀ completely covered by the abdomen, lying in a cavity formed by the latter—*D. caecata*.

1. *Dermatophilus penetrans*

(Fig. F, and Pl. IV. Fig. 28)

As Chigue, Chego, Chigoe, Chigger, Migua, Nigua, Pico, Pique, Tschike, etc., in :

OVIEDO, *Coronica de las Indias, Lib. ii.* p. 14 (1551).

STADEN, *Wahrh. History, Cap.* 33 (1557).

LERY, *Voy. Brézil* p. 168 (1585).

HAKLUYT, *Princip. Navigat.* p. 449 (1598-1600).

ABBEV., *Hist. Miss. Maraynan* p. 256 (1614).

LAET, *Beschr. West Ind.* p. 6 (1630).

BOUTON, *Etabl. Franç. Martinique* p. 91 (1640).

MARCG. and PISO, *Hist. Nat. Bras.* p. 249 (1648).

LIGON, *Hist. Isle Barbados* p. 109 (1657).

TERTRE, *Hist. Gen. Antilles* ii. p. 353 (1667).

ROCHEF., *Hist. Nat. Mor. Antilles* p. 272 (1668).

GAGE, *West Indies* p. 374 (1677).

SLOANE, *Voy. Nat. Hist. Jamaica I. Intr.* p. 124 ; II. p. 191 (1707-25).

FREZIER, *Relat. Voy. Mer. Sud* p. 316 (1717).

CATESBY, *Nat. Hist. Carol., Florida and Bahama Is. II. App.* p. 10. fig. 3 ♂ (1743) (*Pulex minimus cutem penetrans*).

BARR., *Nouv. Rel. France Equin.* p. 63 (1743).

ULLOA, *Hist. Viaja Amer. Merid. I.* p. 88 (1748).

BROWN, *Nat. Hist. Jamaica II.* p. 418 (1756) (*Acarus fuscus sub cutem nidulans probosciae acutiotere*).

GUMILLA, *Hist. Orenoko III.* p. 111 (1768).

BANCROFT, *Hist. Guyana* p. 245 (1769).

HARTS., *Guyana I.* p. 105 (1770).

ANTER., *Voy. Calif.* p. 20 (1772) (Mexico).

BAJON, *Mém. Hist. Cayenne* p. 149 (1778).

AZARA, *Voy. Amér. Mér.* ed. WALKER, p. 208 (1809) (not south of 29° lat.).

Latr., *Hist. Nat. Crust. Ins.* XIV. p. 411 (1805).

SOUTHEY, *Hist. Brazil I.* p. 326 (1810).

SACK, *Reise Surinam* p. 239 (1821).

MONTEIRO, *Angola and R. Congo* p. 167 (1875) (this species ?).

Pulex penetrans, LINNÉ, *Syst. Nat.* ed. X. p. 614. n. 2 (1758) ; *id.*, 4th ed. XII. p. 1011. n. 2 (1767) ; MUELL., *Natur.* V. 2. p. 1042 (1775).

MOLINA, *Sagg. Storia Nat. Chili* p. 214 (1782) (Chili, Coquimbo).

DOBRIZH., ed. KHEIL, *Hist. Obipont.* II. p. 439 (1783) (Paraguay).

FABR., *Mant. Ins.* ii. p. 314. n. 2 (1787).

SCHWARTZ, *Kon. Vet. Ac. Handl.* IX. p. 46. t. 2 (1788) (names : Ton, Pico, Sico, Nigua, Chique, Chigoe, Chigger ; first scientific account).

GMEI., *Syst. Nat.* I. 5. p. 2924. n. 2 (1790).

- FÄHR., *Ent. Syst.* IV. p. 209. n. 2 (1794).
 RODSCH., *Medic. Bemerk. Essequibo* p. 307 (1796).
 OKEN, *Lehrb. Naturg.* iii. p. 402 (1815).
 LATR., in *Determin., Nouv. Dict. Hist. Nat.* XXVIII. p. 251 (1819) (probably not congeneric with irritans).
 POHL, *Reise Brasil.* i. p. 106 (1821).
 HUMBOLDT, *Voy. Nouv. Cont.* VII. 19. p. 250; 20. p. 129 (1820-22).
 DURMER., *Consider. Ins.* I. 54. f. 4, 5 (1823);
 KIRBY and SPENCE, *Intr. Ent.* I. p. 102 (1828).
 ST. HILAIRE, *Voy. Rio Janeiro* I. p. 35 (1830).
 POHL and KOLLAR, *Brasil. Vorzähl. Läst. Ins.* p. 8. fig. (1832).
 ST. HILAIRE, *Voy. Brésil* I. p. 228 (1833).
 LUCAS, in *Guérin, Dict. Pitt. Hist. Nat.* II. p. 163. t. 105. fig. 1, 2 (1835).
 RENG., *Reise Paraguay* p. 274 (1835) (long account of habits).
 WATERT., *Mag. Nat. Hist.* IX. p. 290 (1836) (Guiana, habits).
 DUGES, *Ann. Sc. Nat.* (2). VI. p. 129. t. 7 B (1836) (first scientific account of morphology).
 VOLLM., in *Gistlé, Fauna* p. 274 (1837) (abstr. of RENGGER's account).
 SELLS, *Trans. Ent. Soc. Lond.* II. p. 195 (1839) (Jamaica).
 BLANCH., *Hist. Nat. Ins.* III. p. 633 (1840).
 GERVAIS, *Hist. Nat. Ins. Aptères* III. p. 368. t. 49. fig. 11 (1844).
 GOUDOT, *Ann. Sc. Nat.* (3). III. p. 224, footnote (1845).
 TSCHUDI, *Reiseskizzen aus Peru* I. p. 310 (1846).
 SCHOMBURGK, *Reise Brit. Guiana* p. 122 (1847).
 LUCAS, in *Orbigny, Dict. Hist. Nat.* X. p. 626 (1849).
 GOSSE, *Nat. Soj. Jamaica* p. 177 (1851).
 BURM., *Reise Brasil.* p. 284 (1853).
 MANTEGAZZA, *Amer. Merid.* I. p. 285 (1858).
 MOUSSY, *Descr. Conféd. Argent.* II. p. 52 (1860).
 VIZY, *Rec. Mém. Méd. Chir. Pharm. Milit.* (3). X. p. 306 (1863).
 LABOULB., *Bull. Soc. Ent. France* p. 6 (1867) (Paris; on person from Pernambuco).
 LEBAS, *Anim. Nuisibles* (1867).
 BONNET, *Mém. sur la Puce pénétrante* (1867) (two plates: morph., biology).
 ULLERSP., *Zeitschr. Parasitenk.* II. p. 292 (1870); WRIGHT, *Amer. Nat.* III. p. 386 (1870);
Amer. Natur. XI. p. 756. plate (1877).
 WOOD, in *Watert., Wanderings* p. 386 (1879).
 COMBES, *Le Cosmos* XLIV. p. 424. fig. (1902).
Dermatophilus penetrans, GUÉRIN, *Iconogr. Règne Anim.* p. 12 (1838-40); LABOULB., in *Dict. Encycl. Sc. Méd.* p. 239 (1876).
Dermatophilus penetrans, LUCAS, in *Guérin, Dict. Pitt. Hist. Nat.* VIII. p. 394 (1839).
Sarcophylla penetrans, WESTWOOD, *Trans. Ent. Soc. Lond.* II. p. 19. t. 20 (1840); *id.*, *Introd. Mod. Classif. Ins.* II. p. 493 (1840) (*Sarcophylla* has priority).
 KOLENATI, *Hor. Soc. Ent. Ross.* II. p. 28 (1863).
 KUENKEL, *Ann. Soc. Ent. France* p. 135 (1873).
 WALLIS, *Ver. Naturw. Unterh. Hamburg* II. p. 193 (1875).
 SOYAX, *West Afrika* I. p. 328 (1879) (introduced into Africa in 1872).
 HEINERSD., in *Buchholz, Reis. West Afrika* p. 169 (1880).
 LUX, *Forschungs. Aequat. West Afrika* p. 149 (1880).
 TASCHENBERG, *Die Flöhe* t. 1. fig. 1-3. p. 44, 106 (1880).

- EHLERS, *Zool. Anz.* III. p. 429 (1880) (correction of TASCHENBERG's statement that *Zool. Mus. Gött.* contains foot of lion with *S. penetrans*).
 WHITE, *Cameos from Silver I.* II. p. 426 (1882).
 GUESSFELDT, *Loango Exped.* III. 2. p. 297 (1882).
 SCHIMKEW, *Zool. Anz.* vii. p. 673 (1884) (changes in ♀; rectif. of KARSTEN's account).
 JULIEN, *Bull. Soc. Zool. France* XIV. p. 93 (1889) (W. Africa).
 BLANCH., *ibid.* p. 95 (1889).
 RASPAIL, *ibid.* p. 366 (1889).
 BLANDFORD, *Ent. Mo. Mag.* XXX. p. 228 (1894) (Ningpo, China; on rats, this species?).
 BAKER, *Canad. Ent.* XXIII. p. 20 (1895).
 BLATHWAY, *Internat. Inst. Microsc.* V. p. 345-357. t. 14 (1895).
 JOHNSTON, *Brit. Centr. Africa* p. 368 (1897).
 HESSE, *Centr. Zeitschr.* V. p. 522 (1899) (Distrib. in Africa).
 CLAIR, *Arch. Parasitol.* II. p. 627 (1899) (Madagascar); Joly, *ibid.* (1899); *id.*, *ibid.* III. p. 206 (1900) (Madagascar).
 ENDERL., *Zool. Jahrb., Abth. Syst.* XIV. p. 551. t. 34. fig. 2, 4 (1901).
 RABARY, *La Chique à Madagascar* (1902); ENDERL., *Deutsche Tiefsee—Exp.* III. 7. p. 263 fig. 4 (1903).
 HENNING, *Nat. Wochenschr.* XIX. p. 310 (1904) (Distrib. in Africa).
 BAKER, *Proc. U. S. Nat. Mus.* XXVII. p. 374, 433 (1904).
 MIRANDA, *Bol. Mus. Para* iv. p. 456 (1904).
Sarcopsylla canis WESTWOOD, *Trans. Ent. Soc. Lond.* II. p. 203 (1840) (*nom. nud.*).
Rhynchoprion penetrans, KARSTEN, *Bull. Soc. Imp. Moscou*, p. 72. t. 1. 2 (1864) (best account of morph., anat., and habits); GUYON, *Rev. Mag. Zool.* 1865. p. 295; 1866. p. 64, 111, 326, 359; 1867. p. 7, 208, 276; 1868. p. 25, 70, 101, 171, 312; 1869. p. 70, 212, 284, 325, 384, 413 (*Hist. Nat. et Médic.*; plates of KARSTEN and BONNET reprod.; mostly compil., some original observ.); BAKER, *l.c.* p. 125 (1905).
 ENGEL, *Das Ausland* XLII. p. 1088. fig. 1-4 (1869) (biology).
 GUYON, *Compt. Rend.* LXX. p. 785 (1870) (Mexico); ROULIN, *ibid.* p. 792 (1870) (S. Am.).
 GROUET, *Le Natural.* VII. p. 6, 13 (1885).
 SANCHEZ, *Zool. Medica. Mexic.* p. 150 (1893).
Pulex (*Dermatophilus* GUÉRIN, *Sarcopsylla* WESTWOOD) *penetrans*, HASSELT, *Tijdschr. Ent.* IV. p. 23 (1861).

The morphology of the Chigoe is well-known from the work of KARSTEN, which is far superior to that of BONNET. We abstain from a detailed description of the insect, as the essential features of its structure have been mentioned in the Introduction to the present paper. For comparison with the other species of *Sarcopsyllidae* we figure, however, the fifth tarsal segment (Pl. IV, Fig. 28), and the clasping organs of the ♂ (Fig. F).

For the biology of the insect consult KARSTEN (1864), GUYON (1865-1869), TASCHENBERG (1880), and RABARY (1902), *l.l. c.c.* For bibliography see HUBER, *Bibl. Klin. Ent.* I (1899). The species occurs on man and various mammals in the Neotropical region from Mexico to the northern districts of Argentina, and has been introduced into West Africa during the second half of the last century. It has now

spread on the African Continent from the West Coast to the Lake district, and has also reached Madagascar.

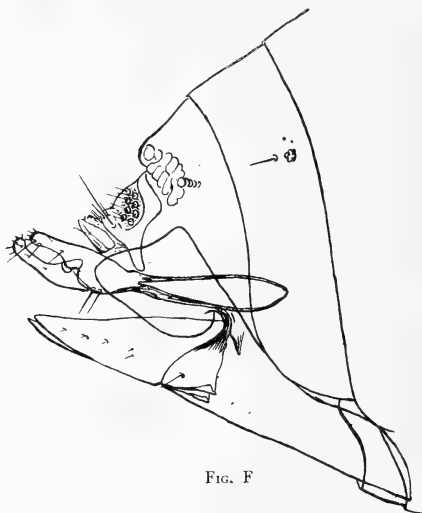


FIG. F

We have the species from :—

British Guiana ;

Sapucay, sixty miles east of Asuncion, Paraguay, collected by W. FOSTER ;

Minas Geraes, collected by A. KENNEDY ;

South Cameroons, collected by W. BATES.

2. *Dermatophilus caecata*

(Fig. D and G)

- ♀. *Sarcophylla calcata*, ENDERLEIN, *Zoolog. Jahrbuch. XIV, Abth. f. Syst.* p. 548. t. 34. Figs. 1, 3, 5 (1901) (Piracicaba, S. Paulo, off *Mus rattus*; id., *Deutsche Tiefsee—Exp.* III. 7. p. 263. Fig. 5 (1903).

The ♂ is not known.

The oral edge of the head of this species (Fig. G) is longer than in *D. penetrans*, while the genal edge is shorter. The frontal tubercle stands closer to the frontal oral angle. The maxillary palpus is shorter, especially the second segment, the hairs of the palpus being far less numerous than in *D. penetrans*. The eye is small, and is devoid of pigment. The head and thorax of the pregnant ♀ are completely retracted into the swollen abdomen (Fig. D, diagrammatical). The membrane

between the fourth and fifth abdominal segments forms a black ring which encircles, as a kind of wall, an anal cavity in which lie the last six segments. The legs are much less slender than in *penetrans*, and the fifth tarsal segment bears five or six bristles on each side according to ENDERLEIN.

Dr. ENDERLEIN found seventeen specimens (♀♀) of this species in the skin behind the ears of a specimen of *Mus rattus*, which was collected by C. NEHRING, at Piracicaba, Sao Paulo, Brazil. ENDERLEIN's figure 1 is a reproduction of a photograph of the head of the host, the picture showing the parasites *in situ*. We have received two specimens in exchange from Dr. ENDERLEIN and the Berlin Museum both specimens lacking the legs.

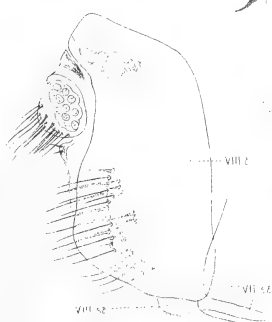
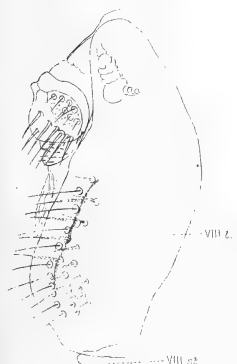
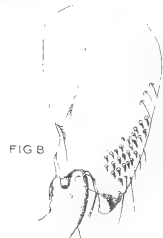
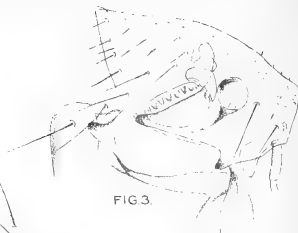
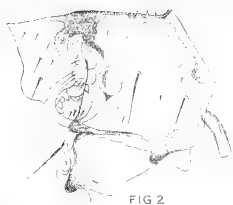
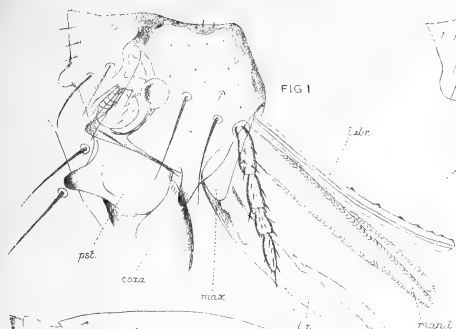


FIG. G

The insect recorded by BIANDFORD in *Ent. Mo. Mag.* XXX. p. 228 (1894) from China as being *D. penetrans* or an allied form may be a species of *Echianophaga*. The specimens, we hear, have unfortunately been mislaid or accidentally destroyed.

EXPLANATION OF PLATES

- FIG. 1. Head of *Echidnophaga gallinaceus*, ♀ ; p. 38 ; *labr.* = labrum ; *mand.* = mandible ; *l.p.* = labial palpus ; *max.* = maxilla ; *pst.* = prosternum.
- FIG. 2. Head of *Echidnophaga liopus*, ♀ ; p. 42.
- FIG. 3. Head of *Hectopsylla psittaci*, ♀ ; p. 47.
- FIG. 4. Head of *Hectopsylla pulex*, ♀ ; p. 49.
- FIG. 5. Head and thorax of *Hectopsylla coniger*, ♀ ; p. 45.
- FIG. 6. Hind coxa, trochanter, and base of femur of *Hectopsylla psittaci* ; p. 47.
- FIG. 7. The same of *Echidnophaga macronychia*, outer side ; p. 31.
- FIG. 8. The same of *Echidnophaga macronychia*, inner side ; p. 31.
- FIG. 9. Eighth, ninth, and tenth abdominal segments of *Hectopsylla coniger*, ♀ ; p. 45.
- FIG. 10. The same of *Hectopsylla pulex*, ♀ ; p. 49.
- FIG. 11. The same of *Hectopsylla psittaci*, ♀ ; p. 47.
- FIG. 12. The same of *Echidnophaga larina* ; p. 35 ; *sty.* = stylet.
- FIG. 13. The same of *Echidnophaga bradyta* ; p. 33.
- FIG. 14. The same of *Echidnophaga gallinaceus* ; p. 38.
- FIG. 15. The same of *Echidnophaga macronychia* ; p. 31.
- FIG. 16. Genitalia of *Hectopsylla coniger*, ♂ ; p. 45 ; *Cl.* = Clasper ; *M* = Manubrium of Clasper ; *sti* = Stigma.
- FIG. 17. The same of *Hectopsylla psittaci* ; p. 47.
- FIG. 18. The same of *Echidnophaga larina* ; p. 35.
- FIG. 19. The same of *Echidnophaga bradyta* ; p. 33.
- FIG. 20. The same of *Echidnophaga liopus* ; p. 42.
- FIG. 21. The same of *Echidnophaga gallinaceus* ; p. 38.
- FIG. 22. The same of *Echidnophaga macronychia* ; p. 31.
- FIG. 23. Fifth hind tarsal segment of *Echidnophaga bradyta*, ♀ ; p. 33.
- FIG. 24. The same of *Echidnophaga macronychia*, ♀ ; p. 31.
- FIG. 25. The same of *Echidnophaga larina*, ♀ ; p. 35.
- FIG. 26. The same of *Echidnophaga liopus*, ♀ ; p. 42.
- FIG. 27. The same of *Echidnophaga gallinaceus*, ♀ ; p. 38.
- FIG. 28. The same of *Dermatophilus penetrans*, ♀ ; p. 53.
- FIG. 29. The same of *Hectopsylla broscus*, ♀ ; p. 46.
- FIG. 30. The same of *Hectopsylla coniger*, ♂ ; p. 45.
- FIG. 31. The same of *Hectopsylla pulex*, ♀ ; p. 49.
- FIG. 32. The same of *Hectopsylla psittaci*, ♀ ; p. 47.



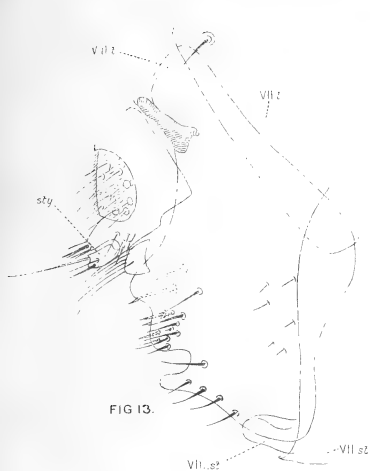


FIG. 13.

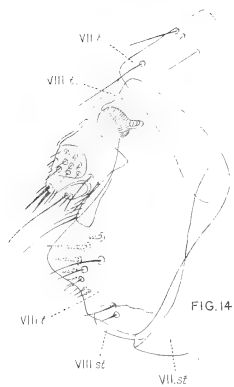
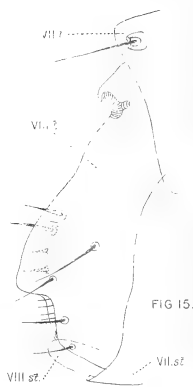


FIG. 14.



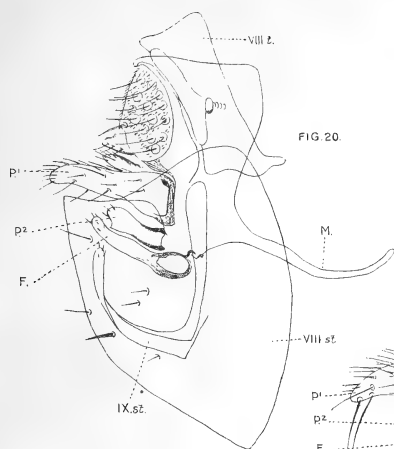


FIG. 20.

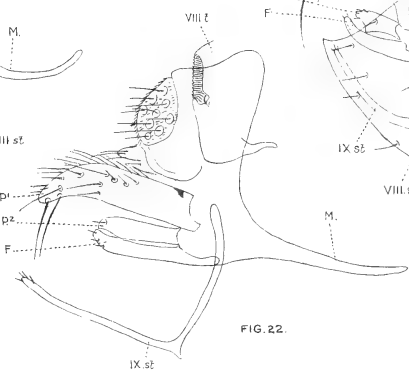


FIG. 21.

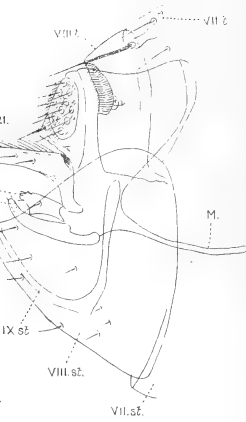


FIG. 22.

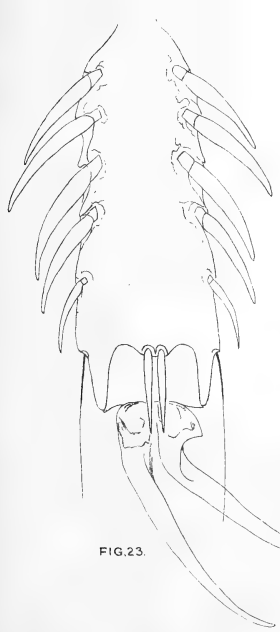


FIG. 23.

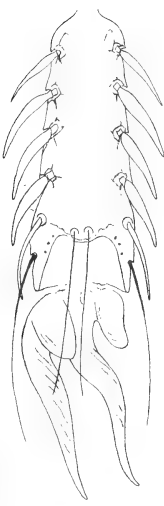


FIG. 24.

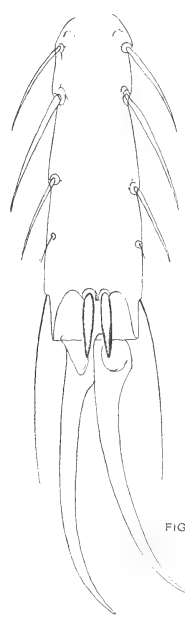


FIG. 25.

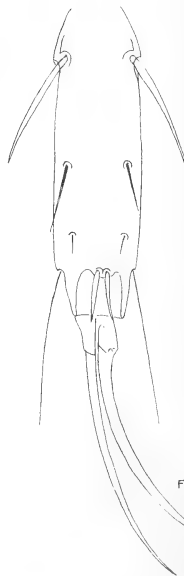


FIG. 26.

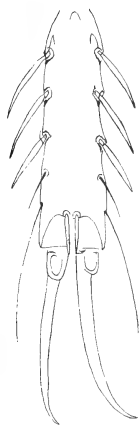


FIG 27.



FIG 28.

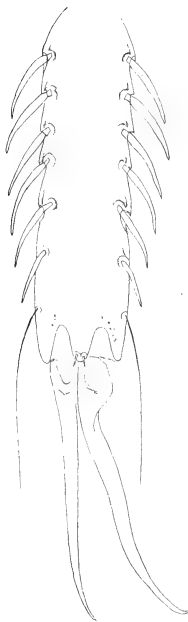


FIG. 29.



FIG 30.

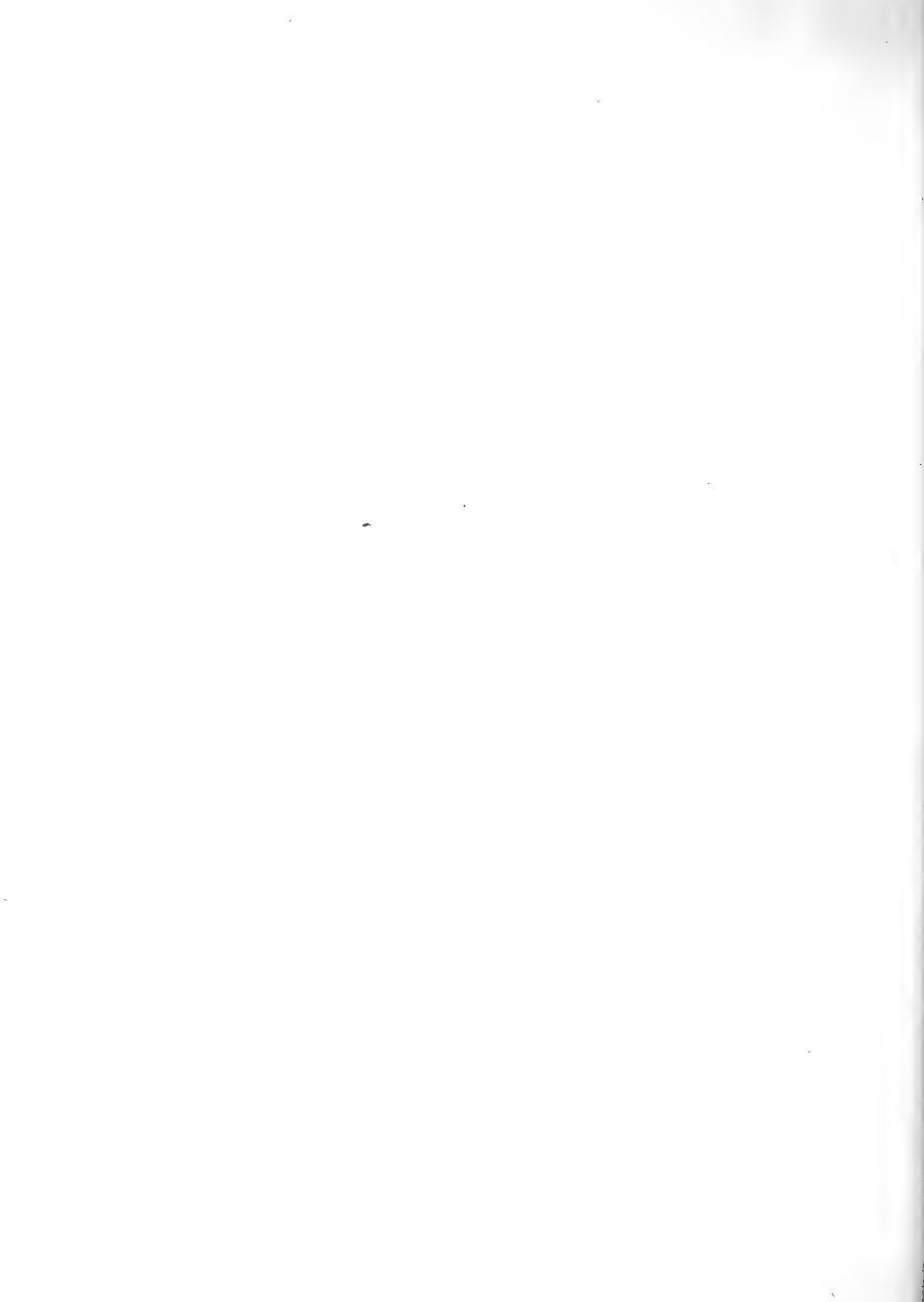


FIG. 31.



FIG. 32.

THE MAIOTIC PROCESS IN MAMMALIA



THE MAIOTIC PROCESS IN MAMMALIA

BY

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AND

C. E. WALKER, F.L.S.

ASSISTANT DIRECTOR

The objects of the present communication are to give as complete and accurate an account, as our present methods will permit, of the maiotic phenomena in mammals: that is to say, of the successive changes which take place during the transformation of pre-maiotic, or somatic, into sexually re-productive cells.

The reasons which make such an undertaking desirable are numerous. In the first place, the existing observations bearing upon the matter are at present widely scattered, both as regards the portions of the maiotic process they refer to, as well as with respect to the types from which the illustrations have been drawn. In fact, curious as it may seem, so far as we are aware, no complete account of the maiotic phenomena in any mammal exists at the present time. The researches of Meves, Borst, Ebner, ourselves, and others have dealt with individual sections of the process, with the origin of the archoplasmic vesicle; the history of the centrosomes in relation to the Spermatozoa; the existence of heterotype and homotype divisions, and the like. But in no existing publication has the whole maiotic process been followed out. In the conjoint work by one of us* and Professor Farmer, the maiotic divisions in mammals were briefly referred to, as coming into the general scheme we were then able to formulate regarding the maiotic process in animals and plants; but the matter was necessarily dealt with in the briefest possible manner, and no attempt was made to indicate in detail the wide divergence which exists between the new interpretation of the processes involved, and the older conceptions regarding the heterotype division, contained in the works of Flemming and others.

It would thus not be undesirable that a full account of our observations upon mammalia should be published merely as a supplement to our former work. But beyond this, the fact that certain features peculiar to the maiotic change have been found by us† to occur as constant cytological peculiarities during the development of malignant growths in man, renders the details of the maiotic change in mammals particularly important at the present time. The formation of archoplasmic vesicles in mammalian sexual cells deserves special attention, for these very definite objects have been shown to be

* The maiotic Phase (Reduction divinus) in Animals and Plants. *Quart. Journ. Micro. Sci.*, Vol. 48, 1904.

† J. B. Farmer, J. E. S. Moore, and C. E. Walker. *Pro. Roy. Soc.*, 1903.

NOTE.—At the last moment we have received a copy of a paper by Prof. F. A. Janssens, "Evolution des Auxocytes Mâles du Batracoseps Attenuatus." We regret that it is at present impossible to deal with this row, though it will be seen that we differ from him materially upon some important points. At least one important stage described by us has not been recognised by Prof. Janssens.

characteristically present in the cells of malignant growths.* Again, it has been ascertained, as will be seen in the sequel, that during the maiotic change peculiarities occur in the position and behaviour of the centrosomes,† and these peculiarities have also been shown to characterise the development of cells during the formation of malignant growths.

Thus in many ways it is desirable that a detailed account of the maiotic phenomena in mammals should be available, and the present memoir contains that part of such a history as is afforded by the study of the development of the male sexual cell. In a future publication it is intended that the development of the female sexual cells shall be similarly treated. But it may be pointed out that although the maiotic phenomena in the case of eggs generally, is vastly more difficult to follow; little, if any, new light will really thereby be thrown upon the subject. The broad features of the development of the egg in mammalia is sufficiently well-known to show already that its history will in all its cardinal features be parallel to the history of the male cells themselves. The only important matter to be readily obtained through an investigation of maiosis in female mammals will be in relation to the probable similarity, or identity, of certain of the so-called yolk nuclei with the archoplasmic vesicles, or Plimmer's bodies, in the male. This matter is at present obscure, on account of the fact that bodies which are unquestionably of diverse origin, are included under the term yolk nucleus, and have not yet been sorted out into different and specific categories.

In dealing with a class of organisms so closely knit together as the mammals, it is not to be expected that there will be much diversity or important differences in the maiotic phenomena of different types, and so far as we know the whole course of events could be successfully illustrated through an examination of any single form. We have ourselves examined the maiotic process in men, baboons, bats, dogs, cats, rabbits, mice, guinea-pigs, hedgehogs, bulls, and the duck-bill platypus. On the whole, among these types, we have found that the guinea-pig is in many ways the best. Yet, as will be seen in the sequel, there are certain stages in the maiosis of this animal which are better illustrated by other types, consequently in what follows we have used the guinea-pig as a mammalian example perhaps best suited to illustrate the maiotic phenomena of the group; but have supplemented this example when necessary by observations based upon the examination of other forms.

For the sake of convenience we have in this, as in our former conjoint work,‡ considered the development of the sexual cells, as naturally divided into three stages:—Pre-maiotic, maiotic, and post-maiotic. The *pre-maiotic period* includes all that series of cell divisions which extends from the first segmentation of the egg to the prophase of the first maiotic (heterotype) division. The *maiotic period* embraces the heterotype and homotype divisions, and the intervening rest; while in mammals, as apparently in all animals, the *post-maiotic period* is only represented by the resting condition of the spermatid, or the egg after the second polar body has been extruded, there being in animals apparently no such post-maiotic divisions as generally

* J. B. Farmer, J. E. S. Moore, and C. E. Walker. *Pro. Roy. Soc.*, 1905.

† See also J. E. S. Moore. *Int. Monat. f., Anat. u. Phys.*, 1894.

‡ *Loc. cit.*

occur in plants. By this means we have, as explained in our former work, a consistent and simple terminology which can be applied with equal precision in the case of any animal or plant. At the same time we entirely obviate the necessity of using the cumbrous nomenclature which has grown up in the literature dealing with this subject, and according to which we find corresponding elements designated by the terms—Spermatocytes of the first and second order; Oocytes of the first and second order; Sporogonia; Oogonia; Spore mother cells; Spores; and the like.

I.—THE PRE-MAIOTIC PERIOD.

For some time after the first segmentation of the egg the cells whose descendants are destined to give rise to the sexual elements, or to form some portion of the animal body, are, so far as their cytological characters go, all essentially similar; as regards the peculiarities of their divisional phenomena, whether the so-called somatic and reproductive tracts become differentiated early, or late, these peculiarities remain constant till the maiotic process is initiated in the reproductive series. Or, as sometimes happens through the appearance of cancer, and under exceptional conditions among plants, meiosis is produced within the elements of the somatic stock. Thus the pre-maiotic sexual cells may be viewed as undifferentiated somatic cells; or conversely, and probably more correctly, the so-called somatic elements can be regarded as differentiated pre-maiotic cells.

All the divisional phenomena of the pre-maiotic cells of the early sexual tract could be equally well illustrated by observations directed upon the ordinary somatic cells of the body, or vice-versâ. And, notwithstanding the fact that the cells of the soma may become specialized, we regard all pre-maiotic elements, whether belonging to the soma or to the anlagen of the reproductive glands, or to the mature reproductive glands, as being essentially similar from a morphological point of view. Maiotic, as well as pre-maiotic, cells may become temporarily specialized; when, for example, archoplasmic vesicles, chromatic bodies, and other structures are present. And post-maiotic cells may become similarly histologically differentiated, as in the case of the spermatozoa. A bundle of spermatozoa is a mass of cells, each of which is more specialized histologically than a cartilage cell, or a connective tissue element, or even most gland cells. Again, the ordinary somatic functions may be discharged by post-maiotic cells, as in the case of the prothalli of ferns, and the peculiar morphological characters of the prothallus can be assumed by pre-maiotic cells in special cases.*

Consequently from such a point of view as the above the question of somatic, or histological, differentiation loses all significance. What remains important are the constantly recurring features of the life cycle of the cells of animals and plants. The three phases, pre-maiotic, maiotic, and post-maiotic: to one of which the cells of any particular tissue invariably belong.

From this point of view the cells of the soma of any animal, and those of the young reproductive series, are both similar, in that they are both pre-maiotic in phase.

* Digby, Miss L. *Pro. Roy. Soc.*, 1905.

In mammals (in vertebrates and invertebrates for that matter) the pre-maiotic cell consists in its simplest form of a nucleus, and its associated cytoplasm. (Figs. 1 and 9.) During rest the nucleus consists of a coarse and irregular network, or foam-like structure, composed of a denser substance (linin) within the shreds and patches of which are scattered in an irregular fashion chromatin granules. In the spaces between the strands of this composite network lies a less stainable substance, and there is generally at least one large, round mass of staining material, forming the so-called nucleolus. The whole nucleus during rest is bounded by a definite membrane.

The cytoplasm consists of a less refractive cytoplasmic mass surrounding the nucleus, and upon ultimate microscopical analysis this substance is found to consist of a finer foam-like structure, or network, between the strands of which there lie granules of various and non-constant properties and sizes.

In mammals, and many vertebrates at any rate, there can usually be differentiated in the resting cell a small patch of denser cytoplasm, generally near some portion of the nuclear membrane. Within this there usually appear two, small, highly refractive, bean-shaped bodies, which under certain conditions stain distinctly, and differ from the other granules to which allusion has been made in that they remain constant in relationship and appearance within the resting cell. These bodies are the so-called centrosomes, and the denser cytoplasm which surrounds them may be conveniently described by using Boveri's term of archoplasm; the archoplasm and centrosomes together being often spoken of as the attraction sphere. (Fig. 9.)

Centrosomes are, however, not always present in cells. They appear to be constant in the tissues of higher animals, and among the lower plants; but they are not present in the cells of many higher plants, either during rest or during the active stages of division. They appear in those plants which possess them, among the Protozoa, and in maiotic cells, as we shall see, to be specially related to motile organs, such as Flagellae. And in general it may be said that the more primitive the type of cell, the more prominent the centrosomes will be. We are, at any rate for the present, inclined to regard them with van Beneden as primitive cell organs; but organs which in numerous instances have become lost.

All the pre-maiotic cells of the body, or indeed those belonging to any part of an animal except the adult sexual glands, multiply chiefly by mitotic division, for although amitosis is present in certain tissues, it is often resolvable, as in the case of Leucocytes, into mitosis, which is, as it were, hurried over, its mitotic origin being still in evidence. True amitosis is relatively rare, and at present obscure, both in its relationships and occurrence. Here again the primitive appears to be the more complex. The segmentation of the egg is produced by mitotic division. The fission of the Protozoa has been shown to be normally mitotic; while amitosis appears in the glands, and highly specialized tissues of the bodies of animals, and plants.

From the first segmentation of the egg, to the definite formation of the sexual glands, the multiplication of the cells forming the whole body is carried out by a series of mitosis, which are all of a similar and pre-maiotic character; and a pre-maiotic division in a mammal may be described as follows:—

PRE-MAIOTIC DIVISION.

When a pre-maiotic cell is about to divide the nucleus becomes finer in texture, and more readily stainable. The coarse granules disappear, and are replaced by evenly distributed, finer, particles. The alveolar structure of the nucleus becomes subsequently coarser and coarser, so that the lining eventually takes on the appearance of a much-contorted ribbon, or ribbons, along which the chromatin is spread. (Fig. 2.) This figure, the so-called spirem, does not follow, as it were logically from the breaking up of the preceding network; but the nuclear contents assume their new form in an arbitrary fashion; for which at present we cannot account. In some cases the spirem has the appearance of a coiled and endless filament; in others this is never fully attained. In any case, however, the spirem stage is succeeded by a phase in which the thick thread work has broken up into a number of segments, as in Fig. 3. In all animals and plants the number of such segments, or chromosomes, is apparently constant, for any particular form, and in mammals this number is thirty-two in man, rats, and guinea pigs, twenty-four in mice.

While the above intra-nuclear changes are going on, others proceed in the cytoplasm. The centrosomes become more conspicuous, and are surrounded by fans of radiations, while eventually they separate from one another with great rapidity, and take up positions on opposite sides of the nucleus. Sometimes in the pre-maiotic division of mammals it is at this period observable that the chromosomes are apparently split longitudinally; but this cannot generally be seen until a later stage. At about the same time the nuclear membrane becomes irregular and disappears; the clear nuclear substance often remaining as a light space round the liberated chromosomes.

The radiations round the centrosomes rapidly increase, extend across this intervening space, and become fixed upon the chromosomes themselves, these bodies gradually taking up an equatorial position, still adhering by their middles to sheafs of spindle fibres. (Fig. 5.) At this period in the guinea-pig it becomes possible to make out that the bent, rod-like chromosomes are longitudinally split, and as the mitosis proceeds the two halves of each chromosome are gradually drawn away from one another towards the centrosomes. (Fig. 4.) Here they collect in a couple of irregular masses of V shaped daughter elements, which are at first arranged in the form of rings (or diasters), the centrosomes lying immediately beyond them. (Fig. 6 and 7.) In a short time the daughter chromosomes become vesiculate, and run into one another, so that eventually they form an irregular nuclear mass at either pole of the dividing cell. (Fig. 7.) These daughter nuclei become eventually surrounded by new membranes, and the centrosomes pass along a groove round their surfaces towards the original equatorial face of each. At the same time the whole cytoplasmic mass of the dividing cell becomes hour-glass shaped, and this character increasing, the cell divides into two, a small residuum of the substance forming a portion of the spindle which originally intervened between the separating chromosomes remaining visible in either cell, and apparently going to form the condensed mass round the centrosomes, or archoplasm. (Fig. 9.)

The nucleoli of such pre-maiotic cells become altered in appearance during division, sometimes breaking up into fragments, which disappear in the cytoplasm. In other instances they persist, and are visible in one or both of the daughter cells for a considerable time. After the daughter cells separate, the nuclei gradually pass back again by insensible degrees into the condition of complete repose originally possessed by the parent form. (Fig. 8 and 9.)

Such, then, is the character of the pre-maiotic cell division of mammalia. It is a process by which the permanent cell constituents, nucleus, sphere, and cytoplasm, are accurately halved, and their sundered moieties eventually re-constructed into two similar elements in the place of one. Substantively each daughter cell is a miniature of the original parent, and the process of division may go on rapidly, as during segmentation, so that the ultimate products are highly reduced images of the original egg; or as during the later growth of the embryo and during the replacement of tissue in the adult body, each daughter of division may grow again to its original size before a subsequent mitosis.

OUTLINE OF THE DEVELOPMENT OF THE MALE SEXUAL CELLS.

In the male sexual glands of mammals before the maiotic process intervenes, and throughout the rest of the body, except in those abnormal cases where malignant growths are superimposed upon the ordinary course of development, the elements which fill up the testicular tubules have been produced from the original blastomeres by repeated divisions of the above within maiotic type. During the first onset of the maiotic change cells lying within the mass filling up the tubules pass into the maiotic condition, and these are eventually discharged as Spermatozoa. The tubules, when mature, become converted into hollow pipes of connective tissue, lined inside with a single layer of pre-maiotic elements. These latter, by continuous divisions, give off internally layer after layer of cells that pass immediately through the maiotic change, eventually become shed into the lumen of the tubule as mature spermatozoa.

In an adult tubule there are, however, besides the layer of pre-maiotic sperm-producing elements, cells which are of a different character. These are the so-called foot cells, and although their origin is by no means as clear as it might be, their function is undoubtedly connected with the maintenance of future crops of Spermatozoa.

In the adult mammalian tubule the cells of the pre-maiotic layer have ill-defined walls, and in some instances it is suggested that the whole of this layer consists in reality of a nuclear syncytium rather than a pavement of individual cells. Moreover, in portions of this layer there exist nuclear figures, which certainly suggest amitotic budding. That is to say, appearances which would seem to indicate that at certain times the cells of the pre-maiotic layer are multiplied by amitosis before passing on into the later stages. The suggestion of amitosis in the pre-maiotic layer in mammals is of great interest from a theoretical point of view, and it is in conformity with appearances observed during the study of the periodical maturation

occurring in amphibia.* We would, however, at present go no farther in this matter, as the work upon amphibia is incomplete.

In the adult mammalian tubule we have then a hollow pipe, lined inside with a layer of pre-maiotic sperm cells, and between these are interspersed a number of foot cells, represented red and grey respectively in figures on Plate VII. On the inner side of this layer there always exist numbers of older elements, which in the figure have been left uncoloured, and will be dealt with later. In such a tubule it will be found that at certain points individual cells, and patches of cells belonging to the pre-maiotic layer, are undergoing mitosis, and that this division is always of the pre-maiotic type. Moreover it can often be seen that at each such division of the pre-maiotic elements one of the daughter cells passes somewhat inwards towards the interior of the tubule, and then enters immediately upon the maiotic stage (Fig. 55). Not infrequently cells belonging to this series are seen which contain one, two, or even four nuclei, and it seems probable that the syncytial mass of cytoplasm has not divided up along with the nuclei: multi-nucleate masses being the result. This inner layer of nuclei coloured blue (Figs. 55 and 56) grow at first slowly in size relatively to the elements in the pre-maiotic layer. Subsequently, however, they grow much more rapidly, and at the same time they assume a distinctly chromatic and granular appearance; this change in reality marking the onset of the maiotic transformation. Such cells are, as a matter of fact, entering upon the long prophase of the first maiotic heterotype division (Fig. 56). When these cells have obtained the dimensions represented in (Fig. 56) they divide and give rise to daughter elements lying in the position represented in (Fig. 57). Subsequently the latter elements again divide, producing the second maiotic (homotype) division. These last products occupy the position represented in (Fig. 58), and without further division are transmuted into groups of spermatozoa, their connection with the foot cells becoming at the same time obvious (Fig. 58).

Such then is a brief outline of the stages in the maiotic transformation as it occurs in the adult mammalian tubule during Spermatogenesis, and it remains for us now to consider in detail the various maiotic phases.

THE FIRST MAIOTIC (HETEROTYPE) DIVISION.

The nuclei which are about to enter upon the prophase of the first maiotic division become finally granular and chromatic, and after at first containing one or two large nucleoli† are seen to possess several scattered about the interior of the nucleus. Towards these chromatic centres the chromatic reticulum is curiously centred, as in Fig. 10.

In mammals the appearance and arrangement of these chromatin centres is highly remarkable and interesting. They correspond to the structure which in 1904 we called the "chromosome anlagen," visible in the rest, and prophase of the pre-maiotic cells of *Periplaneta*. They are also similar to the bodies ("Pro-chromosomes") subsequently described in the first maiotic prophase by Strasburger, Miyaki, and Overton in a number of plants.

* These observations are contained in a paper not yet published by Miss Embleton. The material was, however, worked out in the laboratories of the Cancer Research, Liverpool University.

† Farmer and Moore, on the maiotic phase (Reduction divinus) in Animals and Plants. *Quart. Journ. Micro. Sci.*, Vol. 48.

‡ See Strasburger, Miyaki, and Overton.

The results of our fresh observations upon mammals do not agree with those of the three last-named authors upon plants. They are, on the other hand, exactly in accord with and merely extend those already published by us in conjunction with Prof. Farmer upon the maiotic process in general (*loc. cit.*). The present detailed re-investigation of the synaptic phases in mammals being closely parallel with the similar observations recently published by us in relation to the synapsis in Triton.

In the earliest condition in which it is possible to distinguish the cells that are passing into the maiotic phase, from those of the pre-maiotic layer, it is found that the nuclei have acquired a closer and more chromatic reticulum. Within each there are to be observed several chromatic centres (Fig. A). In many cases it is seen that the chromatic centres are double, or treble, or made up of even more parts of the same size (Figs. A).

From these chromatic centres, the thread work of the nucleus radiates into its substance; and it can often be seen that from each chromatic centre two threads wander off into the general tangle of the incipient spirem. In the cell represented (Fig. A) it will be seen that the number of the components of the chromatic centres varies from 1—5.

In a very large proportion of such cells, in the guinea pig, it is, however, found that the number of chromatic centres is 8, and that each is made up of two parts. This gives to the centres an appearance of duality which is undoubtedly that referred to by Strasburger and his pupils.

Shortly after the stage just described the chromatic network, or fine spirem, contracts into the well known synaptic figure represented in (Fig. B); and this contraction seems to be brought about by the chromatin centres migrating to one side of the nucleus as is seen in the figure.

In both this and the earlier stage the whole of the nuclear threadwork is seen to be centred upon the chromatin bodies, and these become massed together in the manner represented in (Fig. C). In (Figs. B and C) the spirem is seen to be also gradually unwinding; or opening out, into the characteristic loops shown in (Figs. C and D).

Now through the later stages it is not difficult to persistently follow these loops until we see them finally each become individually converted into one of the synaptic gemini (heterotype chromosomes); and since the number of gemini in the guinea pig is sixteen, it follows, there being usually 8 chromatic centres, that these latter each represent the ends of a couple of the sixteen loops.

Their frequently double appearance is due in the first place to the fact that at this stage they tend to be aggregated in pairs: although subsequently they become all dissociated, and even the ends of the loops deviate in the coarse spirem figure as we shall see. (Figs. D, E, F.)

It will be observed that the sequence of events is at this period by no means simple, and the phases of the synapsis so far as we have now gone may be conveniently elucidated by a diagram, wherein only two double and one triple chromatin centres and their associated loops are drawn. (See next page.)

* Moore and Embleton. On the Synapsis in Amphibia. *Proc. Roy. Soc.*, 1905.

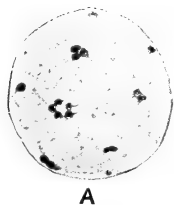


Fig. A.—Early prophase of 1st Meiotic Division from Testis of Guinea pig, showing Chromatin centres.

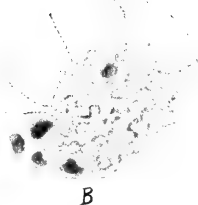


Fig. B.—Prophase of 1st Meiotic Division, showing Synaptic Contraction and Chromatin centres.



Fig. C.—Later stage of Synaptic figure than *B*. The loops are still unsplit.



Fig. D.—Later stage of Synaptic figure. The loops are beginning to show double beading, and the Chromatin centres are separating from one another on the surface of the nuclear membrane.



Fig. E.—Later stage, showing the formation of the coarse spireme through the complete separation of the Chromatin centres. The threadwork shows the double-beading and splitting.



Fig. F.—Later stage, showing the split threadwork of the loops, the split extending to their ends.



Fig. G.—Still later stage, showing the formation of the gemini (heterotype chromosomes) out of the split loops. Two of the gemini show the joint between the two premeiotic chromosomes of which each is formed.

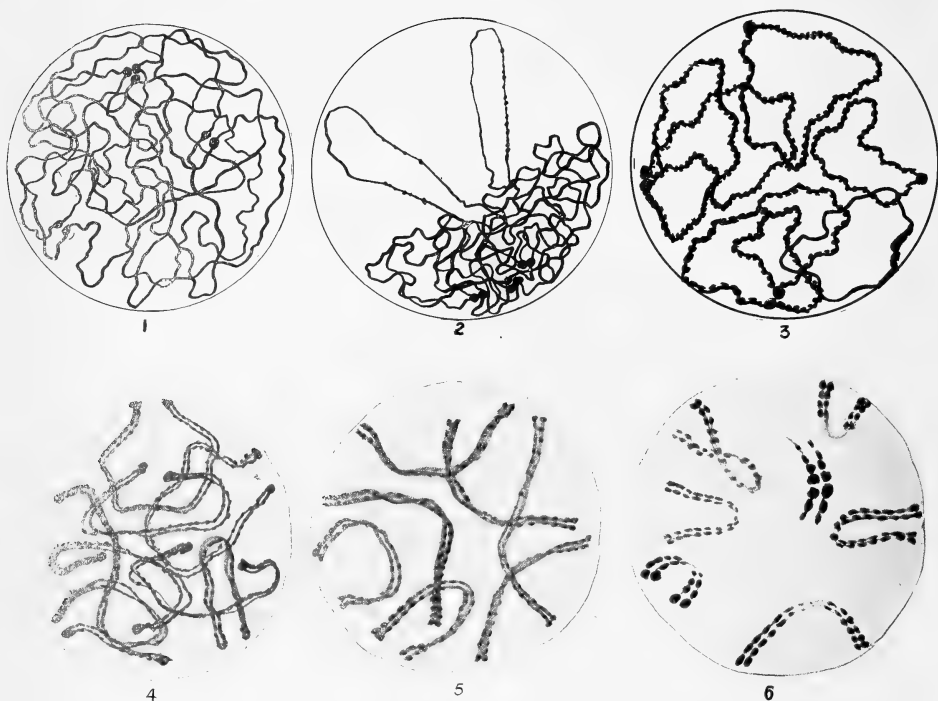


Diagram of the first meiotic prophase in the Guinea pig, wherein only seven loops are represented :—

1. Early spireme and chromatin centres at the ends of the loops. The chromatin centres are in groups of two and three.
2. Synapsis.
3. Later phase where the chromatin centres have separated and one is breaking apart on the right.
4. Later stage where the ends of the loops are all broken apart and the thread is split.
5. Still later stage.
- 6.—Final stage, the loops contracting to form the gemini (heterotype chromosomes). Several of the loops show the joint in their middle, representing the point of opposition of the two premeiotic chromosomes out of which each of the gemini is formed.

At a somewhat later stage the loops assume the arrangement given in (Fig. D). They each consist of a long twisted thread, all ending a few composite chromatin centres that have arisen through the amalgamation into groups of those previously scattered through the nucleus.

The thread consists of linin, along which the chromatin is scattered in the form of irregular granules, as shown in the figure. There is no trace up to this stage of any longitudinal splitting in the thread work. In (Fig. D), however, we have a somewhat later stage than (Fig. C). In this the loops are still seen to radiate from composite chromatic centres, but these are now breaking up again. And in some loops it will be seen that the chromatin is now distinctly arranged in two rows. The loops are, in fact, in the act of assuming the well-known double beaded appearance.

There is no more doubt in the case of these mammalian cells than there is in those of Triton that the double beading of the threads arises through a separation of the chromatin along each individual thread into two rows. But it is questionable whether each of the chromatin granules divides, or whether they gradually become arranged in this manner.

At a later stage (Fig. E) the chromatin centres become separated up, and each is now seen to consist of the peripheral ends of the individual loops.

The double, or split, condition of the thread now extends from end to end of the loops, and this gives to each end, or chromatin centre, on the nuclear membrane, a new appearance of being double.

A later stage is represented in (Fig. F). The double or split nature of the chromatin is still seen. The loops are, however, shortening up to form the adult gemini.

In (Fig. F) it will be seen that these loops are often clearly divided in the middle. Thus at this stage each loop consists of two lengths joined by their ends, and each length is split longitudinally from end to end.

In the guinea pig there are, as we have seen, 32 pre-maiotic chromosomes, and the synaptic loops of the first maiotic division resolve themselves into 16 gemini, so that we are led to conclude that gemini consist each of two somatic chromosomes joined end to end. This conception is fully confirmed by the observations we have made upon the synapsis in Triton, where the coupling up of the pre-maiotic chromosomes can actually be seen during the pre-synaptic rest.

During the time that the coarse spirem is breaking up to form the sixteen synaptic aggregates, remarkable changes go on in relation to the constituents of the attraction sphere. During the synaptic contraction it will be remembered that the centrosomes lay at the centre of an enlarged archoplasmic mass as in (Fig. 14). But at stages such as those represented in (Figs. 18, 19, 20, 21), it is found that the centrosomes migrate outwards from the archoplasmic centre to the surface of that body as in (Fig. 18). Still later they are encountered completely outside the archoplasm, as in (Fig. 20), and at this time it is often noticed that one or both of these bodies has divided, as in (Fig. 21). About the same time it is in some cases—in the guinea pig—possible to discern that from each of the centrosomes there proceeds a delicate protoplasmic thread of extreme tenuity, and only visible if the preserva-

tion and staining of the cell be exceptionally good. These processes seem to correspond to the rudimentary tails originally described by us* in relation to the daughter elements of the first maiotic division in elasmobranch fishes, and subsequently encountered elsewhere in corresponding cells by Meves and others. They are in all cases undoubtedly equivalent to the tail of the Spermatozoa and their appearance in the heterotype prophase of mammalia is distinctly interesting.

While the above changes affecting the centrosomes are in progress other phenomena of a no less important character make their appearance in the archoplasm itself. During the migration of the centrosomes and after, it is seen that within the substance of the archoplasm small clear vesicles appear. They are of minute size, and often in considerable numbers. In each vesicle there is usually to be seen a small dark spot, and the archoplasm presents the appearance represented in (Fig. 21).

Thus, so far as the attraction sphere is concerned, it may be said that the onset of the first maiotic division is marked by a peculiar migration of the centrosomes; the development of rudimentary flagellae in connection with these bodies; and the appearance of archoplasmic vesicles.

When the first maiotic division is drawing to a close, and the cells assume the hour-glass appearance represented in (Fig. 26), the subsequent separation of the daughter elements is marked by the formation of an intervening spindle remnant, which for a time exists as a bridge between the cells. In the centre of this structure there are to be seen one or more stained particles, which have the appearance of thickenings on the original spindle fibres, and correspond to Fleming's intermediate bodies. In all other respects the reconstruction of the daughter cells and the recession of the active nuclei into rest corresponds to what has been described in the case of the pre-maiotic divisions.

THE SECOND MAIOTIC (HOMOTYPE) DIVISION.

The daughter elements of the first maiotic division are represented in their resting condition in (Fig. 27). In all stages after their formation the archoplasm is large, while it seems doubtful in many instances if the centrosomes ever come to lie in the archoplasmic mass. At all events, these bodies in a very early stage are visibly detached from the rest of the sphere, and consequently it is obvious that in this generation there exists the same dismemberment of the constituents of the attraction sphere which marked the onset of the maiotic change. Besides the extra-archoplasmic position of the centrosomes the archoplasm itself becomes again filled with clear vesicles (Figs. 27, 28); while there exists as well the conspicuous irregular chromatic body in the cytoplasm (Fig. 28).

Thus, in this generation, all the peculiar cytoplasmic features which were assumed at the beginning of the maiotic change are again in evidence.

The cells produced by the heterotype division remain in a resting condition a relatively short time, and the onset of the second maiotic (homotype) division is ushered in, so far as the nucleus is concerned, by the formation of chromatic

* Moore. On the Spermatogenesis in Elasmobranchs. *Quart. Journ. Micro. Sci.*, 1906.

condensations, which foreshadow the chromosomes of the subsequent mitosis. These, in the guinea pig, are sixteen in number. No true spirem appears to be formed, and the best description of the process is to say that the chromatic granules become at first aggregated in clouds, and after a time into two rows in each. In this way the young chromosomes have the appearance of being longitudinally split (Figs. 27, 28).

At the same time the centrosomes, usually quite near the periphery of the cell, migrate from one another to opposite ends of the cytoplasm. Radiations appear, the nuclear membrane vanishes, and the sixteen chromosomes become attached to the spindle as in an ordinary pre-maiotic division. The individual halves of each separating to form the daughter nuclei in a similar manner.

We have not hitherto been able to observe the formation of abortive flagellae in these cells, as in the corresponding generation of elasmobranchs.

At the close of the second maiotic division the archoplasm, together with its vesicles, disappears, as it does in the preceding generation, and the spindle fibres form in a marked manner once more the bridging structure between the daughter cells represented in fig.

THE SPERMATIDS.

The reconstruction of the cells produced by the second maiotic (homotype) division, which form the final spermatids, is similar to that witnessed in the preceding generation. The centrosomes appear to be dissociated from the archoplasm, and a gradual metamorphosis is inaugurated which terminates in the formation of the mature spermatozoa.

In the present paper it is intended to confine the description of the events which lead up to the production of the mature male element to its earlier phases. In the first place, it is such phases only which appear to be of wide significance. Secondly, our account of these changes will be found in details not to agree completely with the work of Meves; but the differences are not of sufficient magnitude to require special treatment; whilst thirdly, in the work above referred to, the latter parts of the transformation have been so admirably illustrated and followed that any fresh description of them here seems quite unnecessary.

By the time the daughter elements produced by the second maiotic division have come to rest, the archoplasm is of conspicuous dimensions, and the centrosomes may be found in the cytoplasm, sometimes near the chromatic body, sometimes quite on the periphery of the cell (Fig. 32). At an early stage archoplasmic vesicles appear, and these structures rapidly grow to much greater prominence than in either of the two preceding generations (Fig. 35).

At the same time that the vesicles enlarge they decrease in numbers, until one or two only are left in the archoplasm, as in (Figs. 38, 39, 40, 41). In all cases it appears that only one is finally left, and this grows rapidly, presenting a well-marked membrane, as in (Fig. 41). At the same time the central staining mass in the vesicle becomes more pronounced, and from it there grows out a more faintly staining material, which we will call the *intermediate substance* (Fig. 42). About this time the archoplasmic vesicle (Plimmer's body), together with the remaining mass of the archoplasm (residual archoplasm) becomes

attached to the nucleus, where the vesicle and its contents continue to enlarge (Fig. 42). The clear fluid originally filling the vesicle is now gradually displaced by the expanding intermediate substance which grows out from the central staining body until it fills nearly the whole of the vesicular space (Fig. 43). The clear substance is, as it were, forced down upon the nuclear membrane, and forms a clear collar in the manner represented in (Figs. 45, 46, 47, 48). The intermediate substance continues to grow, and finally begins to encroach into the cup-shaped space occupied by the clear substance until ultimately the latter assumes the form of a ring round the nucleus, as in (Figs. 48, 49, 50).

At this time the nuclear membrane gradually disappears over that part of the nucleus which is underneath the ring formed by the clear vesicular substance, and for a time the substance of the vesicle and that of the nucleus seem to be in for communication (Figs. 49, 50, 51). The central staining body of the vesicle also grows, becomes half-moon shaped, and closely attached to the nuclear wall. In like manner the intermediate substance continues to grow, and follows the clear substance over the surface of the nucleus to the point at which the bulging annulus existed, the latter now gradually shrinking (Figs. 51, 52, 53). From the zone round the nucleus now reached by the vesicle fine out-growth proceed in the manner described by Meves, and these ultimately form a hollow tube projecting beyond the opposite pole of the nucleus, and containing the centrosomes, and the base of the spermatic tail.

While the above changes have been going on the centrosomes have come to lie near the nucleus, opposite the vesicle, and from one of them a tail grows out as represented in (Figs. 48—52), both centrosomes, together with the base of the tail becoming eventually enclosed in a tube proceeding from the nucleus as above described.

For the further details of the completion of the spermatozoön the reader may be referred to the above cited work of Meves. It is sufficient for our present purpose to point out that the archoplasmic vesicle (Plimmer's body), after arising in the above manner, constitutes the anterior cap of the spermatozoön, and the archosome, as well as the tubular sheath for the tail.

REMARKS.

For the foregoing description it will be seen that:—

The maiotic phenomena in mammals, so far as the nuclear structures are concerned, conform with the general scheme of this process given in the joint memoir by Professor Farmer and one of ourselves. We here reach, as was briefly pointed out in that publication, a similar result regarding the nature of the maiotic divisions as that obtained independently by Korschelt in the case of *Ophryotrocha*, and in the same year as ourselves by Montgomery, in amphibia. Still later similar results have been attained by Strasburger and others in relation to plants.

In the first maiotic (heterotype) division the synaptic aggregates are formed by the association of pre-maiotic chromosomes, and those in the ensuing mitosis simply separate from one another, the existing longitudinal split in each chromosome taking no part in the division, and persisting in the diastral stage of the mitotic figure.

The reduction of the number of chromosomes in the second maiotic figure is brought about by this peculiar mode of association and separation.

From the first inception of the maiotic change peculiarities are seen in relation to the attraction sphere. Archoplasmic vesicles appear. The centrosomes take up an extra archoplasmic position, and may acquire, apparently at any time, rudimentary tails. These observations, together with those of Meves and others, strongly confirm the position taken up by one of us in 1895 (after the discovery of the rudimentary tail in the daughters of the heterotype in elasmobranchs), that from the first appearance of the chain of maiotic phenomena the cells in all the succeeding generations in animals tend to revert, sometimes actually, and probably always potentially, to the condition of flagellate gametes.

DESCRIPTION OF FIGURES.

Unless otherwise stated the figures are made from the cells of the testis of the guinea pig, and have been drawn under a 2mm. 1.40 n.a. Zeiss Apochrom. 10-inch tube, 180c.

PLATE I.

Fig. 1.—Resting pre-maiotic cell.

2.—Early spirem.

3.—Late spirem, the thread has broken up into the pre-maiotic chromosomes.

4.—Pre-maiotic spindle figure.

5.—Diaster.

6.—Later stage of same.

7.—Later stage of same.

8.—Reconstruction, daughter nucleus returning to rest.

9.—Resting pre-maiotic cell, similar to Fig. 1.

PLATE II.

Fig. 10.—Early prophase of the first maiotic divisions. The nucleus shows chromatin centres.

11.—Synaptic contraction.

12.—Another view.

13.—Another view.

14.—Later stage in the synapsis.

15.—Stage at which the first splitting of the thread is visible.

16.—The contraction opening out to form the coarse spirem figure.

18.—Later stage, the loops contracting up to form the *gemi*.

PLATE III.

19.—A similar stage to 18.

20.—A similar stage.

21.—Later prophase showing the peculiar appearance of the young *gemi*.

22.—Early spindle figure of the first maiotic division.

23.—The same later.

24.—The same stage in a mouse.

25.—Diaster.

26.—Reconstruction nuclei in daughter cells.

PLATE IV.

Fig. 27.—Resting cell before the prophase of the second maiotic division.

28.—Prophase of the second maiotic division.

29.—Spindle figure of same.

30.—Diaster of same.

31.—Daughter cells of the first maiotic division.

32.—Resting spermatid.

33.—Three spermatid nuclei in a single cytoplasm.

34.—Three spermatid nuclei in a single cytoplasm.

PLATE V.

Fig. 35.—Resting spermatids, with remains of spindle between them, and first indications of the archoplasmic vesicles in the archoplasms.

Figs. 36, 37, 38, 39, 40, 41, 42.—Stages showing development of the archoplasmic vesicle.

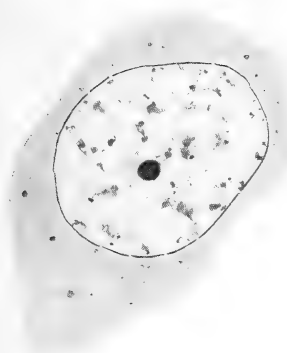
PLATE VI.

Figs. 43, 44, 45, 46, 47, 48, 49, 50, 51.—Stages in the development of the archoplasmic vesicle.

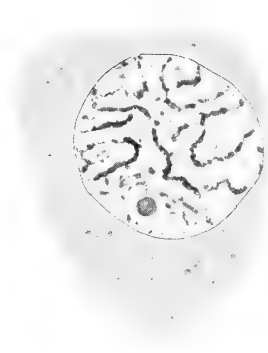
PLATE VII.

Figs. 52, 53, 54.—Stages in the development of the archoplasmic vesicle.

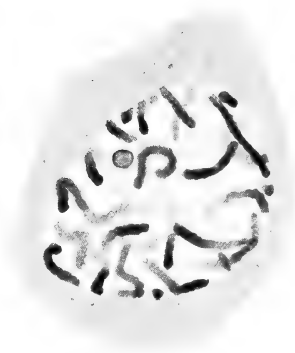
Figs. 55, 56, 57, 58.—Diagrams of spermatogenesis (see text, p. 7).



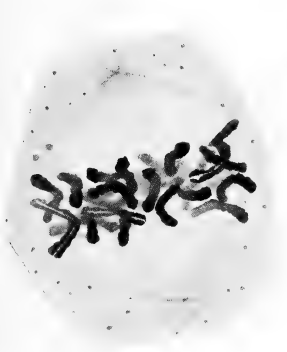
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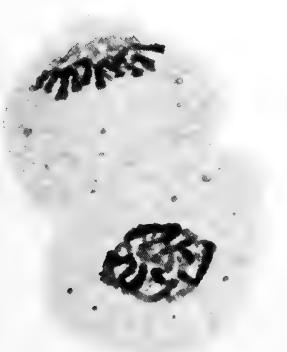
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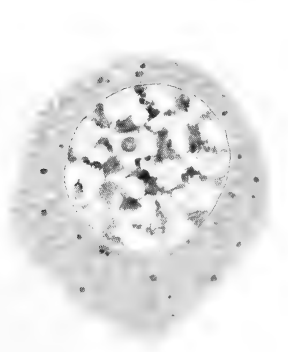
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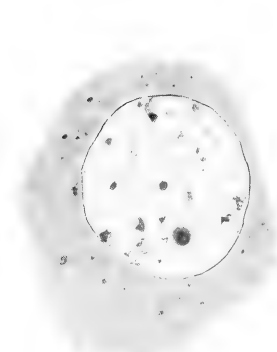
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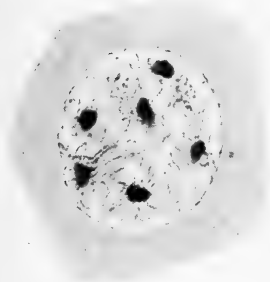


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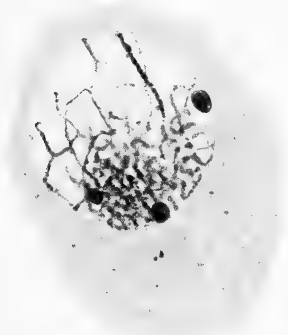


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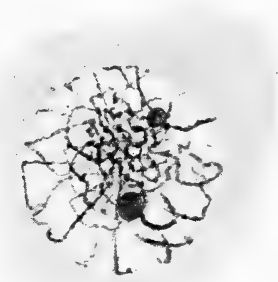




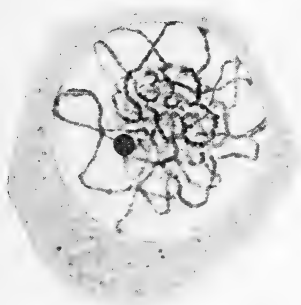
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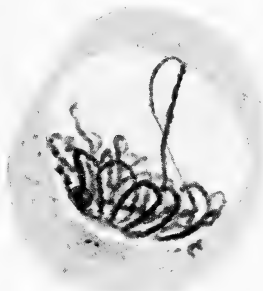
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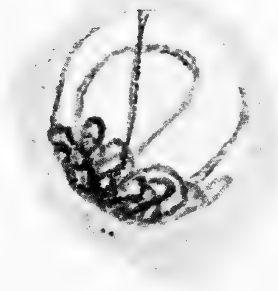
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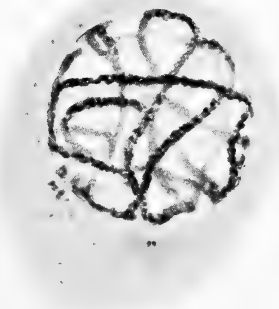
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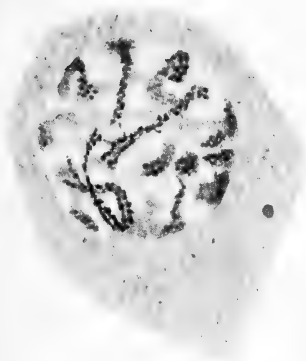


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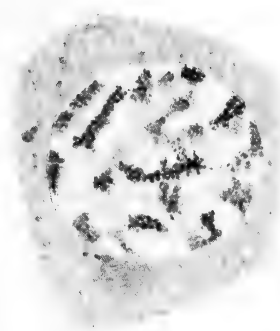


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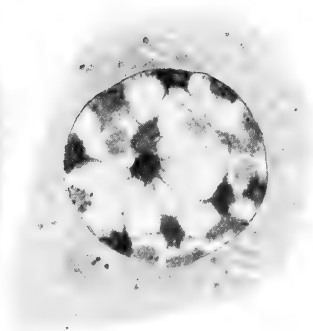




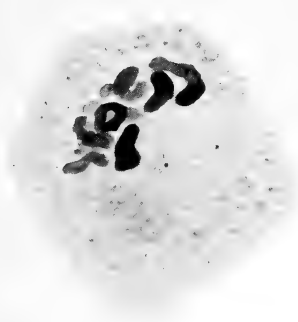
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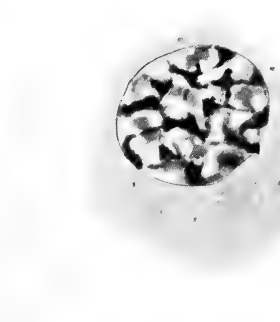
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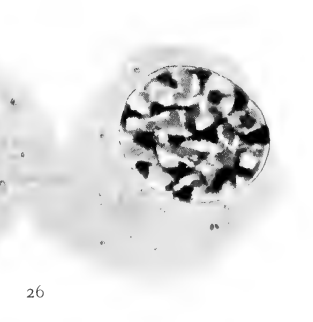
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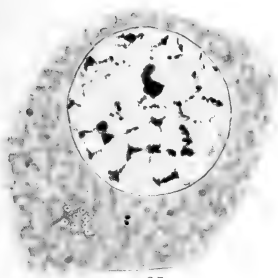


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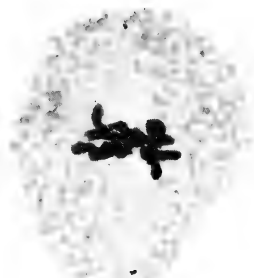




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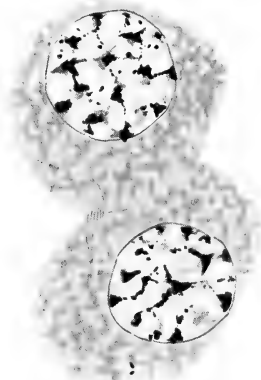
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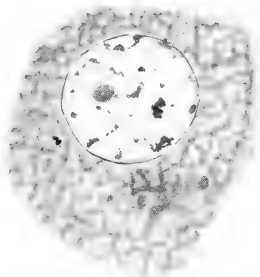
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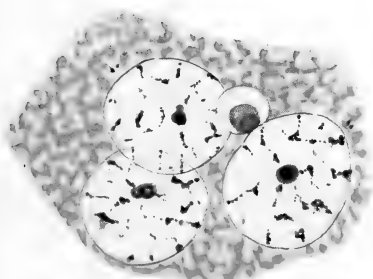
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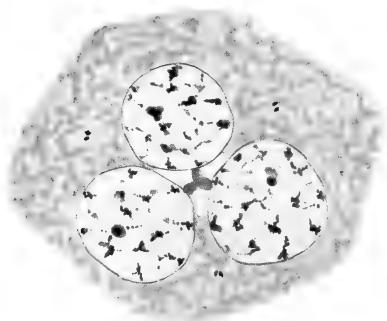
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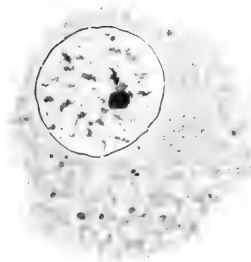


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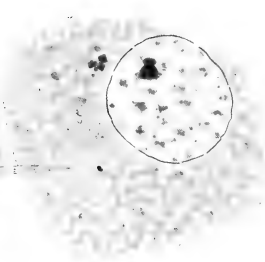


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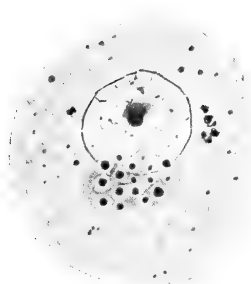
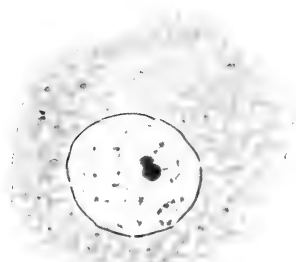




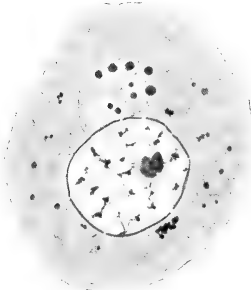
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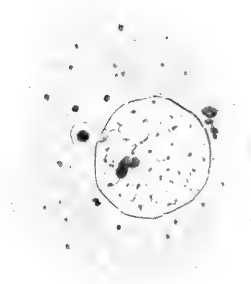
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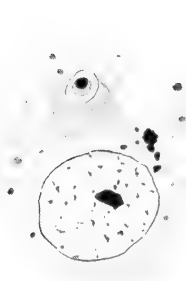
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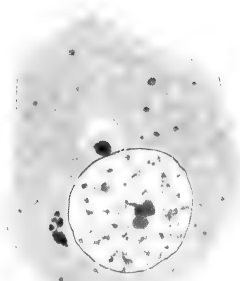
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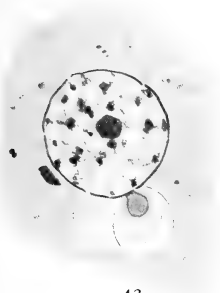


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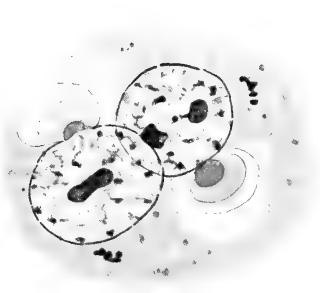


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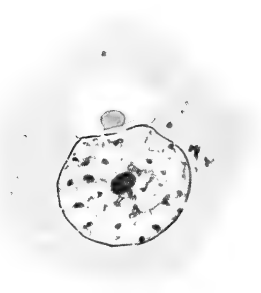




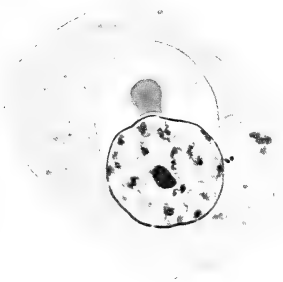
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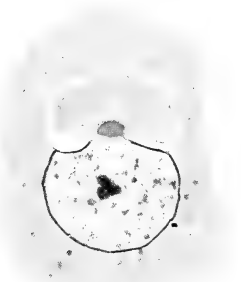
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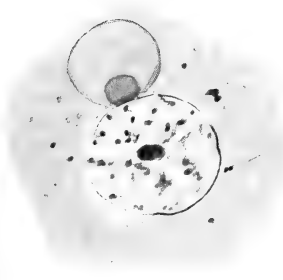
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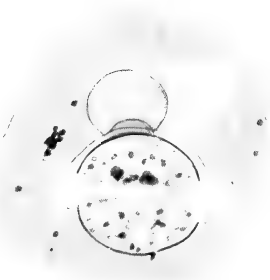
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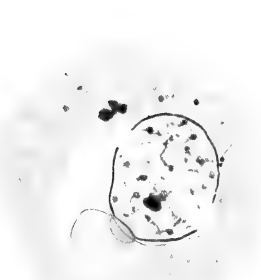
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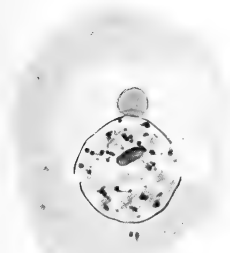


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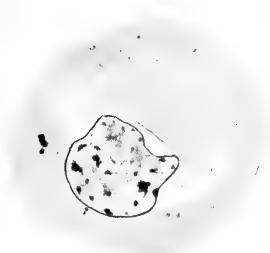


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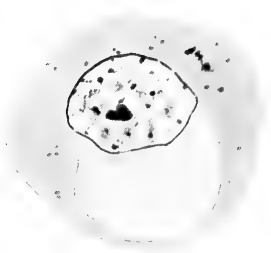




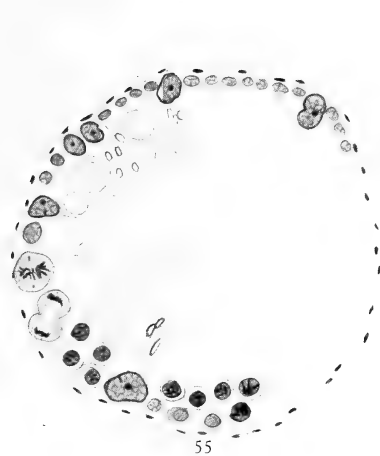
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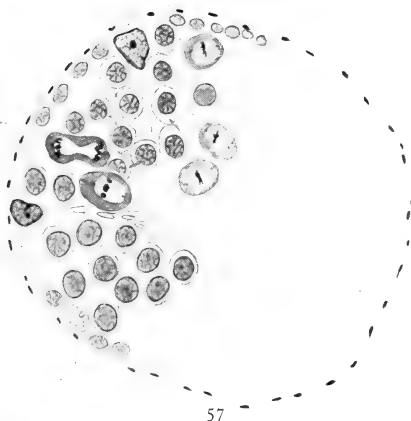
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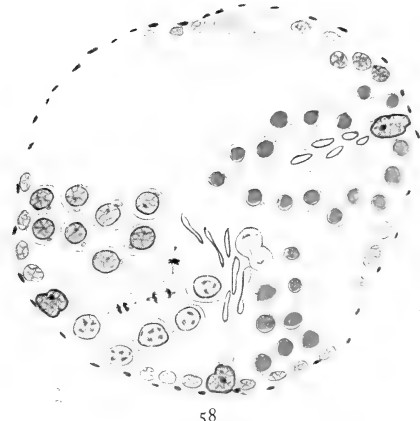
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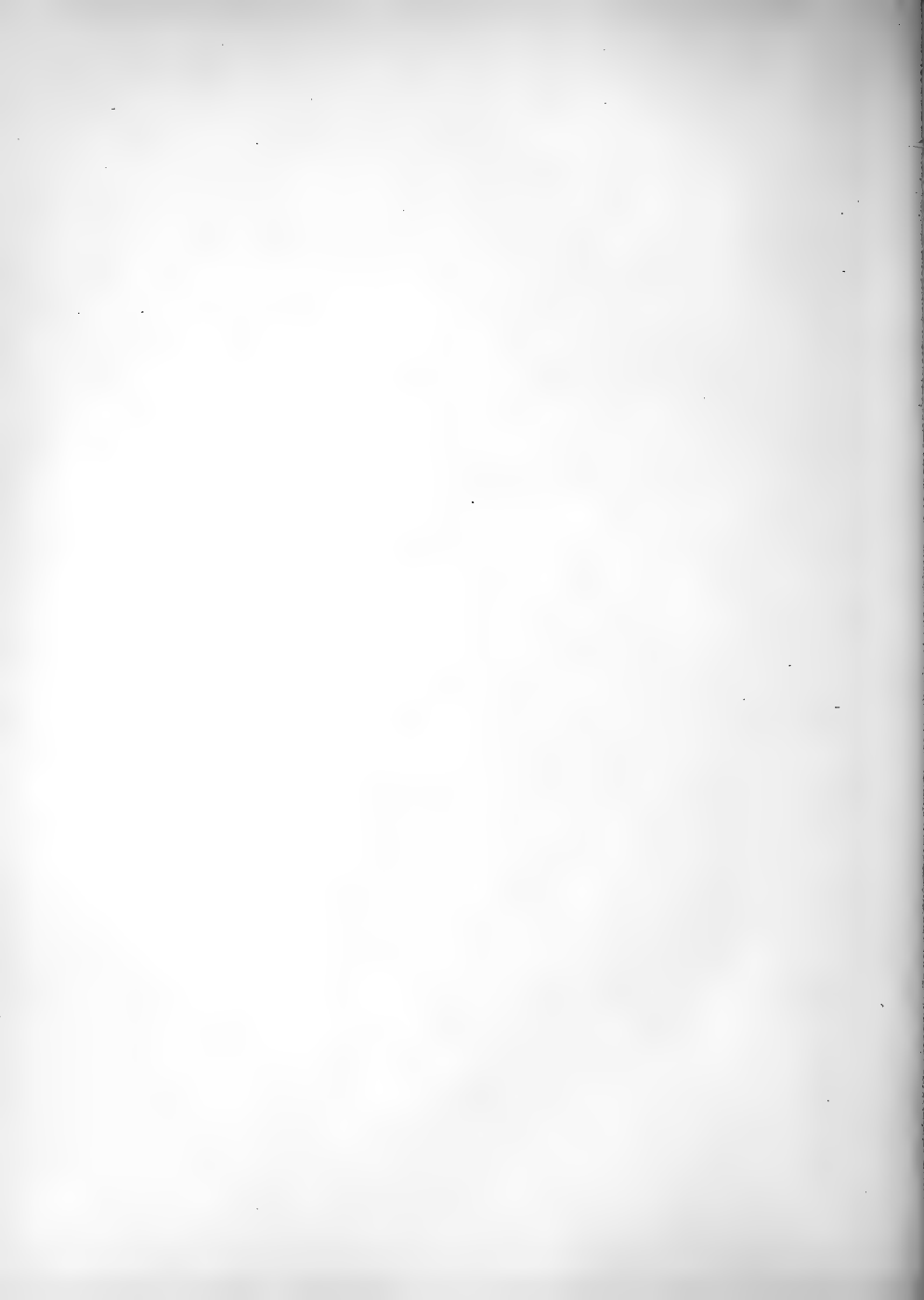
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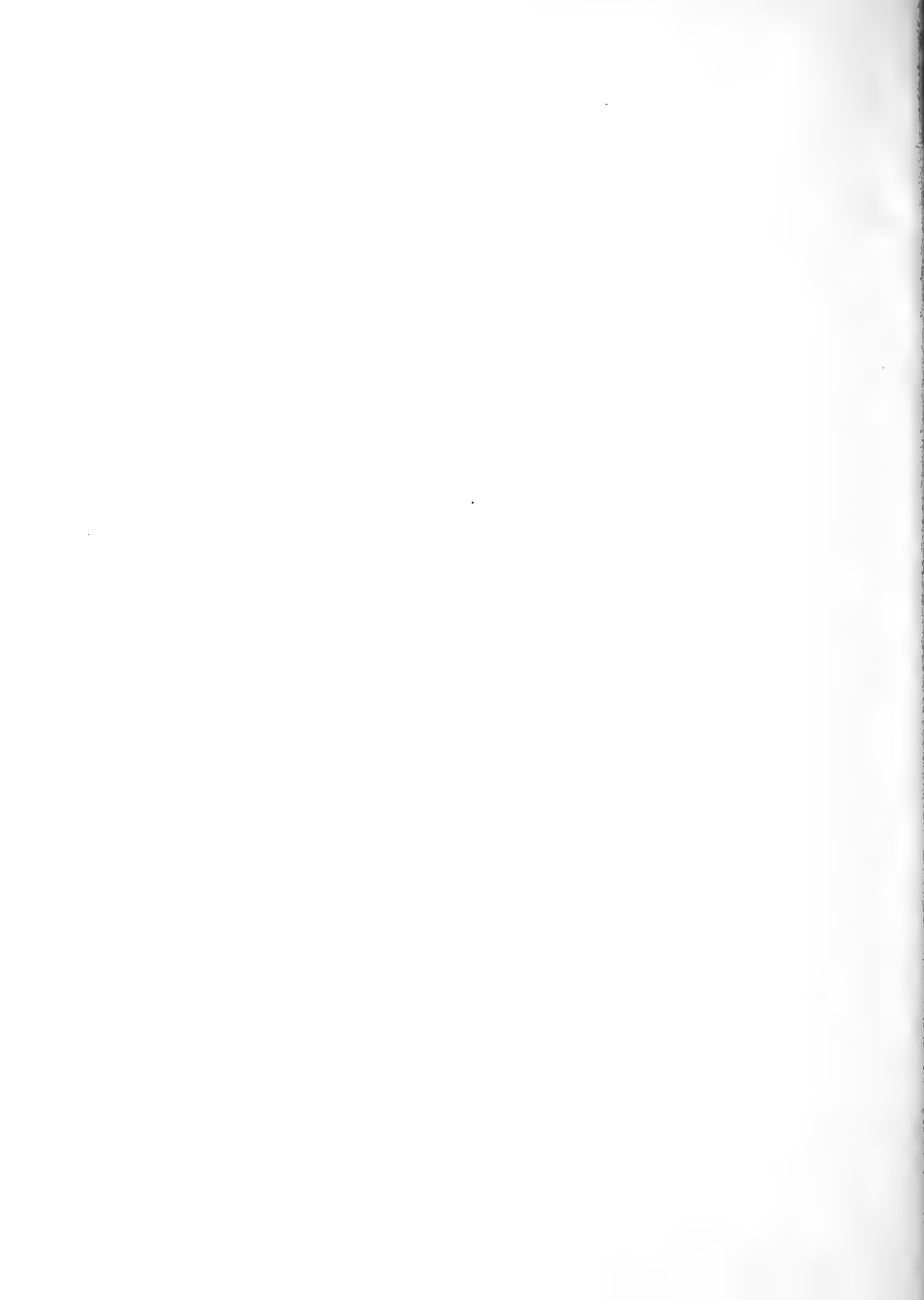
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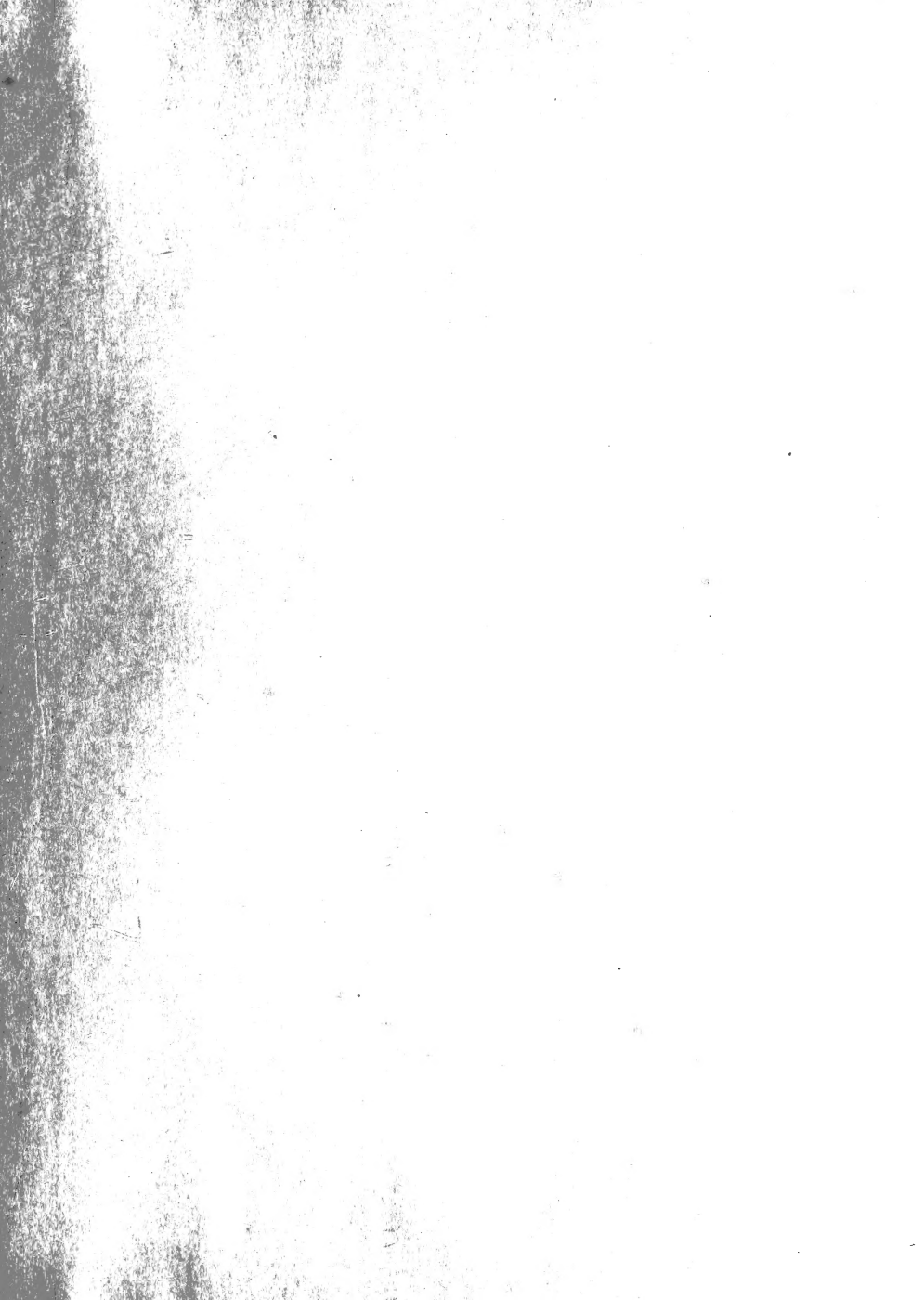
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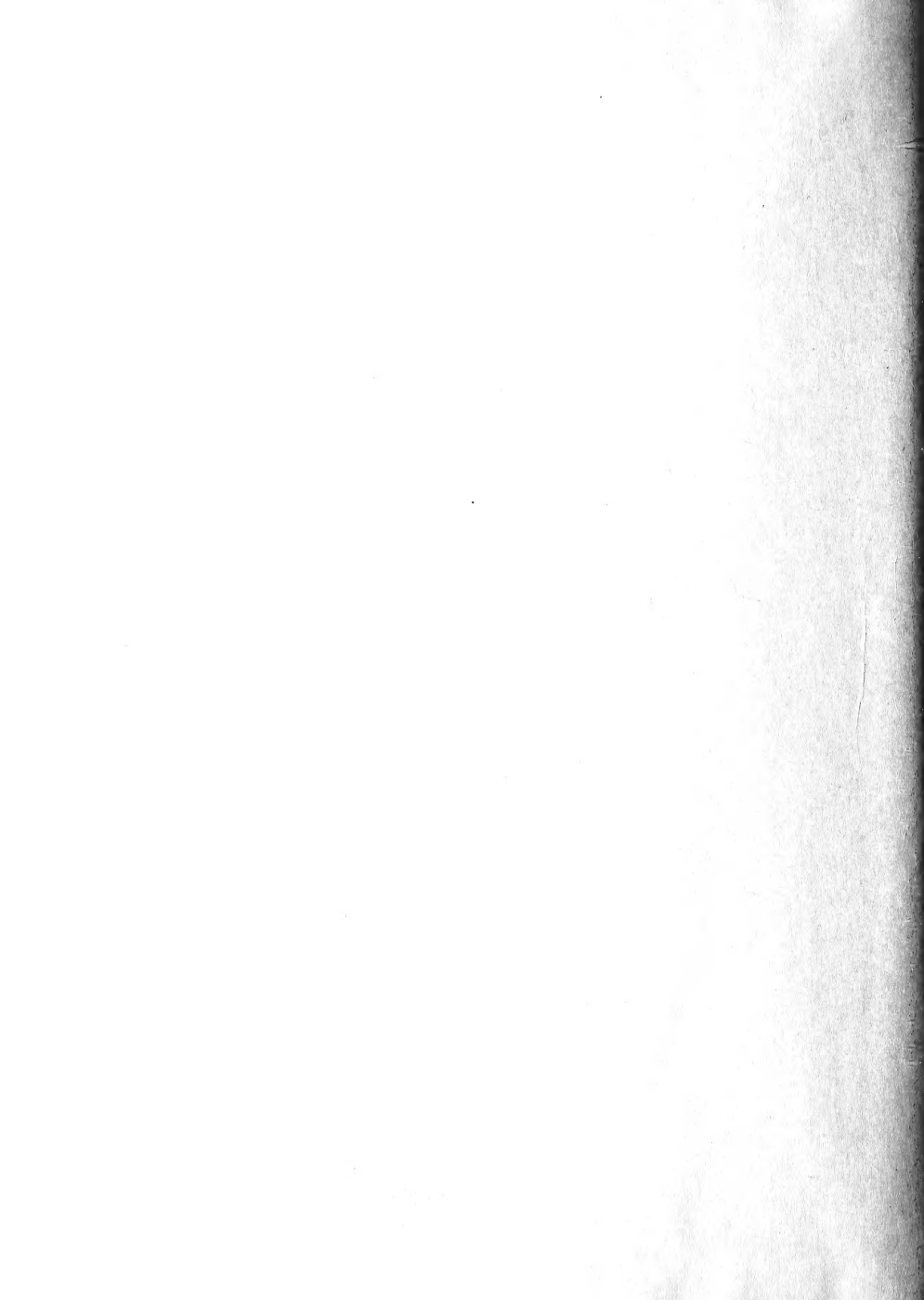
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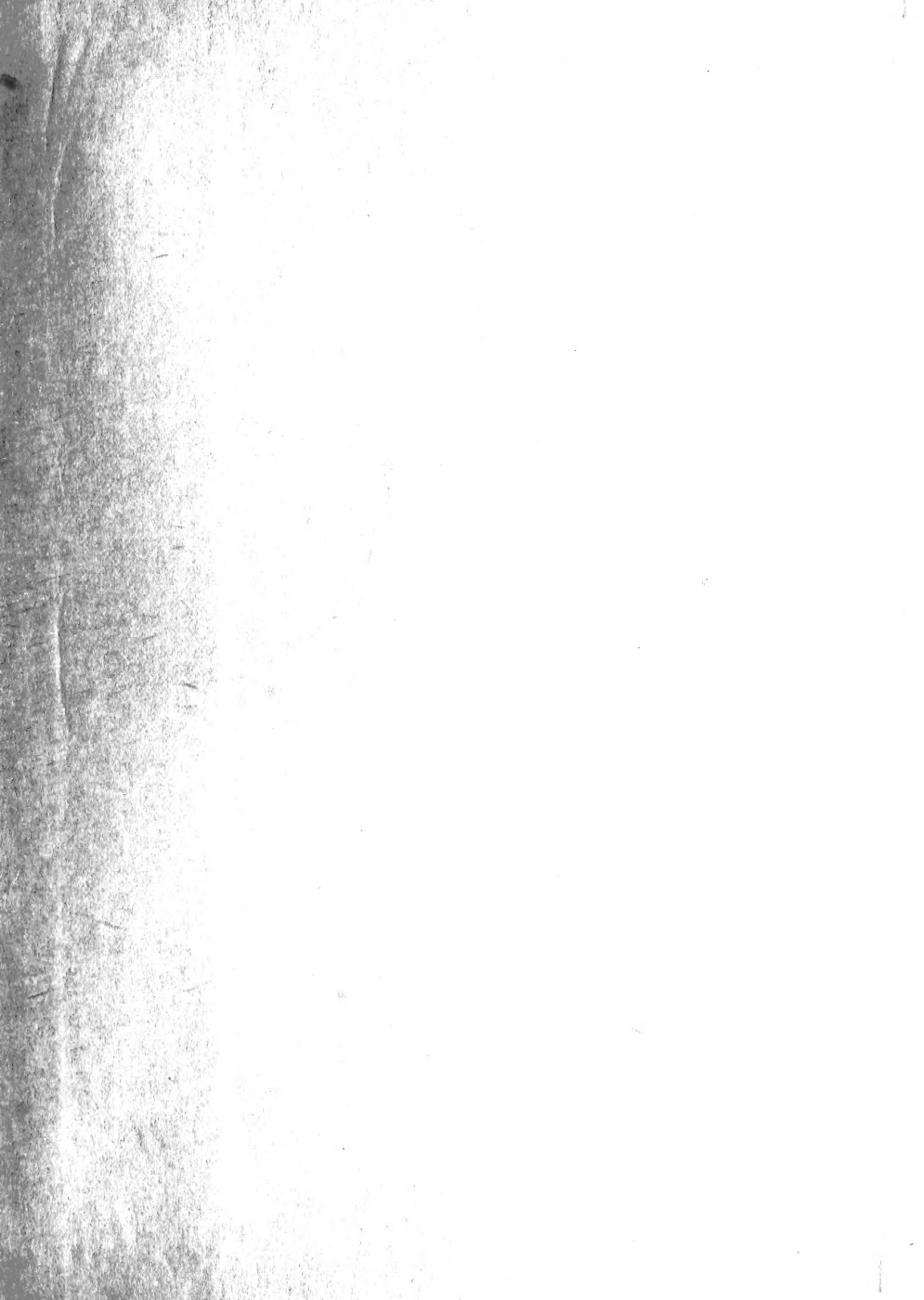
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